Climate, Environment and Malaria during the Prehistory of Mainland Greece

By

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Abstract

Interpretations of osteological remains from mainland Greece during the 1960-1980s led to the suggestion that the most virulent form of malaria, *Plasmodium falciparum*, was prevalent between the Mesolithic and Late Bronze Age (c. 8700 cal. BC-1100 cal. BC). Although disregarded over the past decade, the theory has regained support in recent years from osteological, epidemiological, environmental and DNA studies. However, the presence of this strain of malaria in prehistoric Greece remains controversial.

This thesis evaluates 1) the palaeoclimatic conditions of the Aegean between the Mesolithic and Late Bronze Age and 2) the palaeoenvironmental conditions of three archaeological settlements, with the aim of ascertaining whether the climatic and environmental conditions were as conducive for *P. falciparum* and the mosquito vectors as the osteological evidence suggested. Equal consideration is given to the so-called 'lesser strains' of malaria, *P. vivax* and *P. malariae*, the significance of which is considered to have been underestimated in previous studies.

This thesis is dedicated to:

my mother, Lucienne Forster, who made it all possible and kept me sane with threats of fresh air and exercise

and

to my much missed grandmother, Maisie Morgan.

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On a more personal note, I would like to thank my family, especially my step-father John, my grandmother, Sheila and my partner Paul, for proof reading, critical analysis ("its ok-I just don't see the point of it") and for feigning interest wherever necessary. Many thanks to Bob for introducing me to the fascinating world of malaria; you also helped me to deal with the sharp learning curve that accompanies a transition from an archaeology department to a medical school. I am forever grateful.

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It made the whole process just *so* much more enjoyable….

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Abbreviations:

Latin names of floral and faunal species are followed by the name of the initial author of the study and, if applicable, the date of identification. The following abbreviations are used:

Adans. Adanson.

Erxl. Erxleben.

Desf. Desfontaines.

L. Linnaeus.

Mill. Miller.

Scop. Scopoli.

Vill. Villars.

The common name of floral and faunal species is given in brackets following the Latin nomenclature. The species will subsequently be referred to by whichever name is more commonly recognised.

The names of the *Anopheline* vectors and malarial *Plasmodiae* are abbreviated as follows:

A. maculipennis: Anopheles maculipennis

P. falciparum: Plasmodium falciparum

P. vivax: Plasmodium vivax

P. malariae: Plasmodium malariae

"Everything about malaria is so moulded and altered by local conditions that it becomes a thousand different diseases and epidemiological puzzles. Like chess, it is played with[…] few pieces, but is capable of an infinite variety of situations"

Lewis Hackett 1937: 266.

Chapter One:

Malaria in Prehistoric Greece: Background to the Study

The search for malaria is highly significant to the archaeological understanding of everyday life in early societies. "Perhaps the most important of all diseases which afflict humanity" (Ross 1902: 26), malaria has, in recent years, been responsible for 247 million cases and one million deaths a year across the globe (WHO 2009). The consequences of infection extend far beyond the debilitation of the individual; known as the disease of poverty, malaria carries a heavy social and economic burden that can limit development and progress. The significance of such an affliction amongst the early populations should not, therefore, be underestimated.

The history of malaria within the Aegean has been much debated since the identification of the life-cycle of the disease during the late 19th century by Sir R. Ross (1902); subsequent studies into literary, osteological and genetic data have attempted to ascertain the importance of this disease on early civilisations. W. H. S Jones (1907; 1909) was the first to suggest that Greece was afflicted by the most virulent strain of malaria, *Plasmodium falciparum,* during early history, concluding from literary evidence, such as the Hippocratic texts[1], that the disease was prevalent by the 5th century BC. The theory, although unpopular due to his assertion that the disease was responsible for the moral degeneration of the Greeks, has largely been accepted by succeeding scholars as proof that a strain of malaria was present in the Aegean at this time; however the debate continues as to whether the texts refer to *P. falciparum* infections or to a less virulent strain such as *P. vivax* (Grassi and Feletti, 1890) or

[1] The literary evidence for malaria has been considered in great detail elsewhere and will not be considered in this study (Jones 1909; Bruce-Chwatt *et al.* 1980; Sallares 2002; 2004).

P. malariae[2] (Laveran, 1881) (de Zulueta 1973; 1994; Bruce-Chwatt *et al.* 1980; Sallares 2002).

The advancement of osteological studies during the 1960s gave rise to a far more expansive and controversial theory. Larry Angel (1966; 1971; 1972; 1973) proposed that certain skeletal lesions, termed *Porotic hyperostosis*, correspond with those caused by a genetic anaemia, specifically β-thalassemia. This condition is the most common genetic disease across the Mediterranean, Middle East, Indian sub-continent and across South East Asia; often predominating in coastal regions (thalassemia being Greek for 'anaemia from the sea') (Clegg *et al.* 1999). There is considerable evidence that this and other forms of genetic anaemia, such as Duffy negative trait, sickle-cell disease and G6PD[3] deficiency, are balanced polymorphisms, where exposure to malaria infections activates a genetic resistance which confers immunity against severe infection (Haldane 1949; Angel 1964; 1966; Bridges *et al.* 2008). Immunity in β-thalassemia is effected through defective hereditary β-globin production, which leads to an excess of α-chains that precipitate in the red cell precursors, inhibiting their normal maturation and survival. Although never entirely precluding infection, this bestows considerable resistance against malaria as the "imbalance in globin chain production [...] produces membrane oxidation [which] injures and kills malaria parasites" (Akide-Ndunge *et al.* 2003; Roberts *et al.* 2003; Bridges *et al.* 2008: 89).

Angel's (1969a; 1971; 1973) osteological studies of prehistoric skeletal assemblages from the Aegean identified a high incidence of lesions, leading him to hypothesise that β-thalassemia was common and, by extension, that malaria, specifically the *P. falciparum* strain, was

[2] The fourth strain of malaria, *P. ovale* (Stephens, 1922), has never been endemic within the Mediterranean and cannot be considered as a potential disease burden for the early societies of Greece (Bruce-Chwatt 1980).
[3] Glucose-6-phosphate deficiency.

endemic[4] within Greece between the Mesolithic period and the Late Bronze Age[5]. The skeletal markers caused by β-thalassemia are most severe in homozygotes[6], a condition otherwise known as 'Cooley's anaemia' or β-thalassemia-major. Homozygotes develop severe anaemia in the first year of life and generally fail to thrive; by 2 years of age 90% of individuals are severely symptomatic and require transfusions; life expectancy for untreated cases is less than 5 years (Bridges *et al.* 2008). Individuals suffer from retarded growth, pathological fractures and facio-skeletal changes. The skeletal changes are caused by the precipitation of α-chains, which damage the membranes of the red blood cells, leading to their destruction within the bone marrow; this causes massive hypertrophy of the bone marrow, which will expand up to 30 fold and consequently develop a pronounced porosity. This occurs in a) the facial bones, often causing the protrusion of the upper jaw, b) the long bones, producing cortical bone thinning; as a consequence fractures are common and c) the crania. The latter is highly evident in radiographs, showing a thickened diploë with perpendicular bone trabeculae (figure 1.1) (Bridges *et al.* 2008).

Conversely, heterozygotes for β-thalassemia (referred to as β-thalassemia minor), who have inherited only one abnormal gene, are often asymptomatic with minor skeletal changes and longevity is normal. The skeletal lesions are similar to those of homozygotes, expressed through an expansion of the cranial diploë and pitting of the crania but are, however, far less pronounced. Individuals usually present only slight anaemia, although the condition can

[4] Endemic malaria is defined as the constant incidence of both the disease and transmission patterns over successive years with no appreciable fluctuations. Seasonal patterns can however occur.

[5]

Archaeological Period	**cal. BC**
Mesolithic	8700-7000
Neolithic	7000-3300
Bronze Age	3300-1200/1100

After Manning 1995; Andreou *et al.* 1996; Perlés 2001. Raw ^{14}C yr BP/cal. BP/cal. BC dates for each site are listed in chapter three.

[6] Where the individual has inherited abnormal genes from both parents.

worsen through pregnancy (Sobti *et al.* 2006; Bridges *et al.* 2008). Homozygous individuals, although immune to severe malarial infection, have a greater likelihood of dying from the anaemic condition; heterozygotes, however, have a significant selective advantage for surviving malarial infections, which will increase the prevalence of abnormal haemoglobin genes in the population (Clegg *et al.* 1999; Weatherall 2008).

Angel (1964; 1966; 1971; 1972; 1973) proposed that the skeletal changes linked to β-thalassemia matched those seen in prehistoric assemblages, thereby indicating that early populations had been exposed to infection by *P. falciparum*. These lesions, termed *Porotic hyperostosis*[7] are defined by a pitting or porosity of the cranial vault (*Cribra cranii*) and are found in conjunction (although not exclusively) with porosity of the orbital areas *(Cribra orbitalia*) and of the long bones. Excessive thickening of the cranial diploë and thinning of the outer layer of compact bone is common, which results in a porous bony surface exposing inner bone; the diploïc thickness can extend up to 10 mm, where Angel (1966) proposed that the average of a healthy adult is c. 5 mm. The frontal bones are often mildly pitted and a raying pattern is occasionally evident. In severe cases extensive hypertrophy of the bone marrow vault is manifested; this causes a 'hair-on-end' appearance which is highly evident in X-rays and is similar to radiological images of untreated β-thalassemia in modern cases (Angel 1971; Ortner 2003; Walker *et al.* 2009).

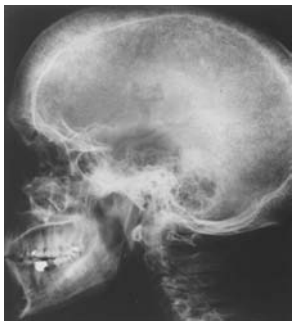


Fig. 1.1: Cranial x-ray of a modern 25 year old homozygote male showing 'hair-on-end' appearance of diploïc space (Georgiades *et al.* 2002: fig. 3B: pg. 1241). These cranial changes have been noted amongst prehistoric assemblages (Angel 1971; Stravopodi *et al.* 2009).

[7] Originally named *osteoporosis symmetrica.*

Angel's theory (1964; 1966) indicated that severe lesions, which were most prominent in sub-adult skeletal samples (under 5 years), reflected homozygous individuals. This suggestion is in keeping with the described progression of β-thalassemia-major, where untreated homozygotes begin to develop severe clinical symptoms during early infancy (c. 2 years of age) and generally die before the age of 5 (Bridges *et al.* 2008). Scholars have drawn attention to rarity of the skeletal characteristics of β-thalassemia-major (severe hypertrophy of the bone marrow and the combination of cranial and post-cranial lesions) amongst prehistoric assemblages from Greece (Stuart-Macadam 1985; 1991; Schultz 2001; Ortner 2003). Angel (1966), however, noted that extensive hypertrophy of the bone marrow is unlikely to be highly frequent amongst untreated cases of β-thalassemia-major, as individuals rarely survive beyond the first few years of life; the short life span would therefore be insufficient for severe hypertrophy to develop. This limited life span, coupled with the selectivity of archaeological sampling, led Angel (1966) to suggest that severe cases would be expected to be infrequent within archaeological assemblages. Trace, slight or healed *Porotic* lesions, he suggested, represent the heterozygote for β-thalassemia, as the genotype causes less severe physiological effects and less damage to the skeletal structure.

Osteological evidence for malaria in early Greece

Based on osteological studies from various sites across the Aegean and the Greek mainland (figure 1.2), Angel proposed that malaria became endemic during the Lower Mesolithic and that the disease flourished throughout prehistory. The frequencies of *Porotic hyperostosis* proposed by Angel (1966; 1971) for the Mesolithic to Late Bronze Age populations at these sites across the Aegean were as follows: Mesolithic: 40%, Early Neolithic: 60%, Late Neolithic/Early Bronze Age: 23%, Middle Bronze Age: 13% and Late Bronze Age: 8%.

Site	Date	Site	Date
Çatalhöyük, Turkey	Mesolithic	Corinth, Argolis	Neolithic
Franchthi Cave, Southern Argolid	*Mesolithic- Neolithic*	*Lerna, Argolis*	*Bronze Age*
Khirokitia, Cyprus	Neolithic	Mycenae, Argolis	Bronze Age
Nea Nikomedeia, Northern Greece	*Neolithic*	Bamboula, Cyprus	Bronze Age
Kephala, Kea	Neolithic		

Fig. 1.2: Table showing sites from the Mediterranean where Angel reported osteological evidence of *Porotic hyperostosis. Italics* represent sites mentioned in the text.

Based on these statistics, Angel (1971) hypothesized a high but declining incidence of the disease in the Aegean. This thesis will focus on Angel's osteological evidence from three coastal sites from mainland Greece: Franchthi Cave from the Southern Argolid, Lerna, sited on the Argive plain in the Peloponnese and Nea Nikomedeia from the Plain of Veria in Greek Macedonia (figure 1.3).

Fig. 1.3. Map of Aegean showing sites mentioned within the text. **1**- Franchthi Cave, Southern Argolid. **2**- Nea Nikomedeia, Veria Plain, Greek Macedonia **3-** Lerna, Argive Plain.

Franchthi Cave, Southern Argolid

The osteological data from Franchthi Cave, lying on the west coast of the Southern Argolid, largely pertains to the Upper Mesolithic period (8700-8000 cal. BC), with some skeletal remains dating to the Middle Neolithic (5900-5300 cal. BC)[8]. Interpretations as to the health of these populations are limited by both the variable preservation and the extremely small size of the assemblages; however, Angel (1969a; *et al.* 1986) considered that the evidence for genetic anaemia was substantial given the limitations. Of seventeen recorded individuals from the Mesolithic, three displayed skeletal lesions which Angel (1969a) associated with β-thalassemia[9]. ***FR 1,*** a male in his mid-twenties, is suggested to have been a heterozygote for β-thalassemia due to the high prevalence of healed cranial lesions. The cranium is heavily marked with distinct porosity and bossing on the frontal, parietal and occipital bones. These measure 9, 8 and 6+ mm respectively, whereas Angel (1969a) proposed that 5 mm is the normal value for a healthy adult, "suggesting a 90% increase in blood-forming tissue as a response to anaemia, perhaps thalassemia" (Angel 1969a: 381). Angel (*et al.* 1986) undertook radiological studies which reflected this hypertrophy of the bone marrow, suggesting an abnormal haemoglobin response as protection from *Plasmodium falciparum*; unfortunately this study has not been published. No post cranial lesions were noted.

Skeleton ***FR 2***, a male in his mid-thirties, showed marked *Porotic hyperostosis* with surface porosity along the lamboid suture and distinct thickening of the parietal, frontal and occipital diploë. These measured 9, 8 and 6 mm respectively, over twice the normal value, leading Angel (1969a) to suggest childhood anaemia, possibly thalassemia, as the primary cause. No

[8] Mesolithic: 10696-10028 cal. BP/ 9430±160 and 8940±100 ^{14}C yr BP. Neolithic: 7778- 7485 cal. BP/ 6940±90 and 6600±250 ^{14}C yr BP (Jacobson *et al.* 1987; Perlés 2001; Reingruber *et al.* 2005). Calibrated with OxCal. 4.1.

[9] The Mesolithic sample is now considered to consist of a minimum of 28 individuals following the discovery of additional human remains amongst the faunal assemblage. There is however no evidence for *Porotic hyperostosis* amongst these latter individuals (Cullen 1995).

postcranial lesions were noted. Mild traces of *Porotic hyperostosis* were also noted in the scant remains of ***FR 67***, an infant of approximately one year, where the frontal bone showed mild bossing and 1.5 mm diploë (Angel 1969a; *et al.* 1986). These samples are considered to date to the Lower Mesolithic; there is no data pertaining to *Porotic hyperostosis* amongst the Upper Mesolithic assemblages.

The Neolithic assemblage was considerably more comprehensive; approximately 115 individuals were identified with a high frequency of child and infant burials. The majority of these samples are, however, highly fragmentary, compromising little more than a bone scatter; the identification of the minimum number of individuals and interpretation as to the health of the population is therefore severely hampered. Angel (1969a; *et al.* 1986) noted marked *Porotic* lesions on three individuals; these were originally dated to the early Neolithic, but have been subsequently re-assigned to the early Middle Neolithic (Vitteli 1993). ***FR 11***, a child of approximately five years, was reported to have notable anaemic thickening on the cranial bones, with *Cribra orbitalia* and vault porosity along the lamboid suture and on the sphenoid. ***FR 12***, a child of approximately eight years also showed notable thickening of the frontal, parietal and occipital bones and traces of *Cribra orbitalia*. Postcranial lesions are not present in either individual; however Angel (1969a; *et al.* 1986) interpreted the cranial lesions as distinct indicators of β-thalassemia. ***FR 21*** is represented by a small cranial fragment, which shows light porosity of the right occipital and thickening of the diploë, which was suggested to indicate borderline *Porotic hyperostosis* (Angel 1969a; *et al.* 1986). Trace lesions were further found in the highly fragmentary remains of ***FR 46*** and ***FR 59*** which Angel (*et al.* 1986) dates to the Middle Neolithic and in ***FR 82*** and ***FR 29***, dated to the Late Neolithic; these latter results, however, remain unpublished.

Angel (1969a; 1971; *et al.* 1986) acknowledged that the sample size at Franchthi was too limited for definite conclusions to be drawn; interpretations as to the health of these

individuals are therefore extremely hypothetical. However, Angel (1969a; 1971) suggested that the frequencies of *Porotic hyperostosis* amongst the Mesolithic assemblage from Franchthi Cave reflected a high exposure to *P. falciparum*. Based on climatic studies, which will be considered further below, Angel (1969a; 1971) suggested that this genetic immunity could not have developed amongst the local populations due to unfavourable climatic conditions preceding the beginning of the Mesolithic period; the malaria parasite and mosquito vector could not have survived and the human population could not, therefore, have been sufficiently exposed for a genetic immunity to develop. It was therefore proposed that both the genetic condition and the malarial strain was introduced by migrating populations and subsequently became endemic in the area. The Neolithic assemblage, although too fragmentary to draw definite conclusions, led Angel (1969a) to suggest a continuing malarial endemicity.

Recent re-evaluations of the skeletal assemblages from Franchthi have, however contradicted Angel's (1969a; *et al.* 1986) hypothesis. Cook (2000) indicates only trace anaemic lesions and only amongst the Neolithic assemblage which, it is suggested, are linked to dietary causes; the "modest levels [...] rule out such exotic causes as [...] malaria and thalassemia as argued by Angel" (Cook 2000: 101). These contradictory results, and the implications for the aims of this thesis, will be considered further below.

Nea Nikomedeia, Plain of Veria, Northern Greece

Nea Nikomedeia is an early Neolithic tell site located on the Veria Plain in northern Greece (figure 1.3). The settlement was occupied on two occasions during the Neolithic period; however the osteological evidence pertains exclusively to the Early Neolithic population

(6700/6500-5800/5600 cal. BC)[10] and the Late Neolithic occupation (c. 5800/5600-5400/5300 cal. BC) is not therefore considered within this thesis (Angel 1973). The skeletal assemblage from Nea Nikomedeia, numbering 105 individuals, revealed an extremely high frequency of *Porotic hyperostosis*, leading Angel (1973) to suggest that malaria was highly endemic during the Neolithic period. Detailed reports on the osteological study, as described for Franchthi, are unfortunately not available; however Angel (1973) does provide overall statistics for the prevalence of genetic anaemia amongst this early population.

Angel reported trace and slight *Porotic hyperostosis* in 36% of 22 adult samples and in 39% of a total of 23 children and infants. Medium to severe lesions occurred in 17% of 23 infant and child remains and in 32% of 22 adult samples, indicating that two-thirds of the total adult assemblage showed some degree of skeletal lesion (Angel 1973). Diploë thickness was on average three times the normal value and several infants displayed post cranial lesions, with extra flaring of distal ends of long bone. One infant, labelled ***43 NN***, showed an inner shell of remodelled shaft within the long bone, where hypertrophy of the red marrow prevented normal development of the bone as the individual grew; this individual was one of four which were suggested to be homozygotes for β-thalassemia (Angel 1966; 1973).

The extremely high prevalence of the condition at Nea Nikomedeia was "more than one balanced polymorphism can explain" leading Angel (1973: 105) to propose multi-causal agents, suggesting that sicklemia, thalassemia, dietary deficiencies and "some other source of anaemia" were combining to create such a high incidence (1973: 105). He proposed, however, that malaria was one of the primary causes of the condition. The skeletal assemblage from Nea Nikomedeia has not been reassessed in light of Angel's (1973) interpretation; however Triantaphyllou (2001) confirmed an extremely high frequency of

[10] 8363-7765 cal. BP/ 7557±91 and 6920±120 ^{14}C yr BP (Stuckenrath 1967; Andreou *et al.* 1996; Reingruber *et al.* 2005). Calibrated with OxCal. 4.1.

severe *Porotic* lesions amongst the assemblage and noted that this may plausibly be linked to genetic anaemia.

Lerna, Argive Plain

Lerna, located on the Argive Plain on the Peloponnese (figure 1.3), was occupied throughout the Bronze Age (2650/2450-2200/2150 cal. BC to 1360-1200 cal. BC)[11]. The skeletal assemblage is particularly comprehensive for the Middle Bronze Age (MBA) (2050/2000-1680 cal. BC)[12], from which Angel (1971) details 234 individuals in comparison with only 27 individuals from all other periods of occupation (Neolithic- Roman) combined. A potential problem with interpretations as to health and disease, as with the other skeletal samples studied by Angel from the Greek mainland, is the disarticulation of the assemblage; a total of two-thirds of the MBA assemblage (157 of 234) is sufficiently well preserved for osteological study, with less than 25% of all sub-adult remains sufficiently complete to assess the overall health of the individual. Furthermore, the MBA sample of 234 individuals represents over twenty generations, which results in less than twelve people per generation. Angel (1971) acknowledges this limitation and chose, for demographic purposes, to treat the assemblage as a single cohort.

Of these 157 individuals, 32 (20%) showed varying degrees of the lesions with 10 (6% of the total assemblage) displaying medium to severe lesions. Five potentially homozygous individuals were identified (Angel 1971). ***Ler 10*** an infant of approximately one year of age displayed an inflated skull vault with marked porosity and thickening of the parietal, occipital and alisphenoid bones. *Cribra orbitalia* was also evident. Post cranial lesions were identified

[11] Early Bronze Age: 4587-4253 cal. BP/ 4070±72-3840±72 ^{14}C yr BP. No radiocarbon dates are available for the Late Bronze Age. (Kohler et al. 1961; Ralph et al. 1962; Manning 1995). Calibrated with OxCal. 4.1

[12] Middle Bronze Age: 3793 cal. BP/ 3520±59 ^{14}C yr BP. Calibrated with OxCal. 4.1. (Kohler et al. 1961; Ralph et al. 1962; Manning 1995)

with a “puffed up appearance” of the lower femoral shaft (Angel 1971: 48). ***Ler 133,*** a child of 1-2 years, displayed marked *Porotic hyperostosis* on both crania and long bones. The parietal and occipital bones were notably thin with considerable pitting and raying of the exterior: these bones, as well as the frontal, malar and the wing of the sphenoid were thickened with unusually porous diploë (figure 1.4a). Angel (1971) further noted post cranial lesions in the femurs.

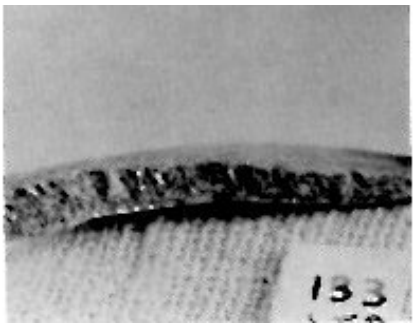


Fig. 1.4a : ***Ler 133.*** 1-2 year old infant crania displaying severely thickened diploë (Angel 1971: Plate XXIII)

Ler 204, an infant under one year, exhibited striking pathological changes; Angel (1971) reported that the parietal bone was thickened and *Cribra orbitalia* was highly evident. Post cranial lesions were also present: the long bones being thicker than average by 10%, while the right humerus contained an inner shell of bone representing the original ‘unremodelled’ shaft. Angel (1971) suggested that this lesion reflected an advanced haemolytic disease, proposing that β-thalassemia as the most likely cause (figure 1.4b).

Fig. 1.4b: ***Ler 204.*** Humerus displaying the inner-shaft (Angel 1971: Plate XXIII)

Ler 81 and ***Ler 103***, both children of 2-3 years, also displayed distinctive *Cribra orbitalia* and pathological thickening of the skull vault (1971).

Angel identified at least four possible heterozygous individuals, displaying either healed or mild lesions; ***Ler 66,*** an adult, displayed healed *Porotic hyperostosis* lesions of medium severity. ***Ler 202***, a newborn, showed bowed radius and tibia and lipping along the ends of the long bones, suggesting severe growth disturbance. Angel (1971) considered that this was a possible indication of β-thalassemia although other causes were plausible. ***Ler 206,*** an infant with raying and pitting on internal parietal, occipital, orbits and the outer surface of the cheekbones, and ***Ler 203,*** a 4 year old infant, showed raying and traces of healed *Porotic hyperostosis*. The latter could again be caused by other sources of anaemia. Very slight or trace lesions potentially linked to anaemia were identified in at least eleven individuals ***Ler 1***, ***3, 18, 48, 71, 72, 102***, ***125***, ***207*** and ***241*** all of which displayed slight porosity, raying of the crania, some in conjunction with *Cribra orbitalia* (1971).

It is worth noting that although the assemblage is strongly biased to the Bronze Age, two of ten skeletons from the Neolithic period also exhibited *Porotic* lesions: ***Ler 220*** displaying healed cranial lesions which Angel suggested represented heterozygous lesions. ***Ler 242***, exhibits far more severe lesions; the diploë displayed severe thickening suggesting severe anaemia and potentially indicating a potential homozygote (Angel 1971).

Angel (1971) proposed that the high frequency of the skeletal lesions within the Middle Bronze Age populations indicated that genetic haemolytic diseases were common; this contention was supported, he suggested, by the high rate of infant mortality within the assemblage. Over half of the 234 individuals (56%) have an estimated age of less than sixteen years, with 84 (36% of entire assemblage) having an estimated age of under one year. This proportion of infant mortality, significantly greater than that he proposed for the Mesolithic or early farming populations in Greece, was suggested to reflect the heavy mortality rate linked to those homozygous for genetic anaemia (Angel 1971). Angel extrapolated from this data that *P. falciparum* was prevalent around Lerna during the Bronze Age.

Angel's interpretations of the osteological evidence

Angel (1966; 1971; 1973) supported his theory of high frequencies of β-thalassemia with brief climatic and environmental reconstructions of the three sites across the Greek mainland. Environmental reconstructions indicated a high malariogenic capacity, with all three sites positioned in low-lying, coastal regions with high water availability; historical malarial records from Greece indicate that Lerna and Nea Nikomedeia in particular are both located within notorious malarial regions, being surrounded by extensive marshland (Balfour 1936; Lividas *et al.* 1941). Angel (1971) hypothesized that the frequencies of skeletal lesions during the chronological periods outlined above were linked to a high environmental capacity, which altered repeatedly between the Mesolithic to Late Bronze Age due to climatic changes and anthropogenic influences.

Angel (1973) suggested that the climatic transition to the "warm Atlantic period" during the Mesolithic would have permitted the introduction of virulent malaria into the Aegean (1973: 104). The wet and warm conditions of this phase would, he suggested, have created marshy territory that would have supported the vector mosquitoes, while the viable temperatures would have facilitated transmission of the parasite. The increase in *Porotic hyperostosis* during the Neolithic and Early Bronze was suggested to reflect a particularly high malarial endemicity, linked to exceptionally wet conditions between c. 7000-c. 2000 BC (c. 8950-3950 BP), the advent of agriculture and the nucleation of human populations. Angel (1966; 1971) suggested that this combination of factors would have simultaneously increased breeding grounds, mosquito densities and the human host groups for *Plasmodium falciparum.* The augmented capacity would therefore result in increased vulnerability to the disease and the autochthonous development of genetic immunity would logically follow.

Angel (1966; 1971; 1973) proposed that *P. falciparum* would have become less prevalent during the Bronze Age due, he suggested, to both a climatic shift and to improvements in farming techniques. While the osteological evidence at Lerna was interpreted as indicating a high frequency of genetic immunities amongst the population; Angel (1971) argued that the transition from the warm Atlantic period to the more arid conditions of the Sub-Boreal period would have limited the potential for malarial transmission (1973). He further proposed that as farmers became more proficient at managing soils and crops, with a reduced use of standing water in ditches that often radiated from springs and other water sources, mosquito breeding grounds would have either been limited or eradicated; farming populations would have consequently been less highly exposed to malarious areas (Angel 1971; 1973).

The climatic data that Angel (1971) referred to is no longer considered apposite; the Atlantic and Sub-Boreal climatic trends do not pertain to the Mediterranean region, but rather to north west Europe (Eastwood 2009, *pers. communication*). Recent advances in the field of palaeoclimatology can provide greater detail of the climatic trends of the chronological period in question and can help to determine the viability of subsequent climatic conditions for transmission; a review of the palaeoclimatic data will therefore be provided in chapter three. The theory of a link between environment and malaria will be reviewed further below.

Recent interpretations of the osteological evidence

It must be noted that there are many caveats to Angel's (1966; 1971; 1973) interpretation of the osteological record. The aetiology of *Porotic hyperostosis* is not as clear as Angel (1966; 1971; 1973) proposed; this has caused considerable debate over the past century and while Angel's (1966; 1971; 1973) theory found some support (Tayles 1996; Lovell 1997; Littleton 1998), the hypothesised link between *Porotic hyperostosis* and β-thalassemia has been largely disregarded during the past two decades. Osteological studies have considered that

acquired anaemia (iron-deficiency), rather than genetic anaemia, causes these skeletal lesions. This hypothesis is largely based on the high frequency of the condition amongst Neolithic assemblages; the coincidental occurrence of *Porotic hyperostosis* and the advent of the agricultural revolution led scholars to suggest that the lesions were linked to a less healthy lifestyle, caused by the transition to sedentary living, aggregation of populations and a dietary shift leading to iron deficiency (Cohen *et al.* 1984; Stuart-Macadam 1985; 1991).

A dietary cause for *Porotic hyperostosis* has, however, been contested in recent years (Lewis 2004; Walker *et al.* 2009; Stravopodi *et al.* 2009). A recent reassessment of Mesolithic, Neolithic and Bronze Age assemblages from eleven sites across Greece have indicated that *Porotic hyperostosis* is in fact "a morphological feature with a multi-factorial aetiology" (Stravopodi *et al.* 2009: 258-259), which exhibits considerable variances across different regions (Schultz 2001; Walker *et al.* 2009). The condition is not indicative of a single disease or condition but is in fact linked to many different diseases and conditions, including genetic and acquired anaemia, scurvy, rickets, periostitis, osteomyelitis, leukaemia, meningioma and metastases (Schultz 2001; Ortner 2003; Lagia *et al.* 2007). The studies, employing histological, endoscopic and macroscopic investigations, therefore show renewed support for Angel's (1966; 1969a; 1971) theory, suggesting that genetic anaemia may have been one of many agents for skeletal lesions in prehistoric Greece (Schultz 2001; Stravopodi *et al.* 2009).

Research into the relationship between *Porotic hyperostosis* and environment from Neolithic and Bronze Age sites across the Aegean and Cyprus has strongly supported Angel's (1966; 1971) environmental hypothesis, showing a definite correlation between low-lying, marshy and coastal sites and high frequencies of the skeletal lesions (Hapiot 2002; 2003; Stravopodi *et al.* 2009). This has led Stravopodi *et al.* (2009) to show tentative support for Angel's theory. It should be noted, however, that this latter study has indicated a different pattern of *Porotic hyperostosis*; despite noting a high frequency of lesions amongst Neolithic

assemblages, Stravopodi *et al.* (2009) question whether the disease, if the main cause, could be considered endemic. Furthermore, where Angel (1971) noted a decrease in the frequency of the condition between the Neolithic and Bronze Age, Stravopodi *et al.* (2009) noted an *increase* in the prevalence of the lesions.

Angel's (1964; 1966) hypothesis regarding *Porotic hyperostosis* may, therefore, be considered plausible; however many limitations to the theory remain. Firstly, the osteological assemblages are small and often extremely fragmentary due to poor preservation, which limits their interpretive value. Secondly, the suggested frequencies of *Porotic hyperostosis* at Franchthi Cave have been challenged by recent studies and are suggested to have been overestimated (Cook 2000; Stravopodi *et al.* 2009); while Triantaphyllou's (2001) reassessment of the skeletal assemblage at Nea Nikomedeia confirmed Angel's (1973) statistical analysis, the former studies may serve to cast doubt on Angel's (1971; 1973) statistics regarding the frequency of skeletal lesions within the assemblage at Lerna. Thirdly, the osteological lesions can only indicate that the population had a history of exposure to malaria; it does not necessarily indicate that the disease was contemporary. Combined with the evidence for a multi-factorial aetiology, research therefore suggests that Angel's statistics (1971; 1973) for *Porotic hyperostosis* and his theory regarding the significance of these lesions must be viewed with caution.

aDNA evidence for malaria

The identification of a multi-factorial aetiology for *Porotic hyperostosis*, although suggesting that Angel's (1969a; 1971) hypothesis is plausible, cannot prove the existence of β-thalassemia amongst early populations. The search for malaria amongst past civilisations has therefore led to ancient DNA (aDNA) analysis, a process which may directly identify balanced polymorphisms from human remains. Studies have however been inconclusive, as

recent analysis of aDNA from Neolithic and Bronze Age assemblages, including Lerna and Nea Nikomedeia concluded that the material exceeds the expected limit for aDNA survival in Greece. Remains from Lerna, dating to the mid- to Late Bronze Age, were found to be recoverable; however, the preservation rate was extremely poor due to the marshy environment of the region, which promotes the degradation of aDNA material (Chilvers *et al.* 2008). The limitations involved in the preservation of aDNA therefore restrict the application of these techniques in the search for malaria amongst the Mesolithic to Bronze Age societies of the Aegean.

A more direct method of identifying the existence of malaria in early prehistory is to isolate *Plasmodiae* DNA from ancient human remains; the different malarial parasites can be distinguished through the PCR (Polymerase chain reaction) of species-specific sequences, a process which permits the amplification, replication and subsequent identification of an aDNA sequence (Taylor *et al.* 1997). This process, although inapplicable within Greece due to difficulties with preservation, has proved extremely successful in the analysis of Egyptian remains dating to the New Kingdom to the Late Period (c. 1550-500 BC). Two separate studies have identified a total of six individuals, including the celebrated Tutankhamun, to be unambiguously positive for *P. falciparum* (Nerlich *et al.* 2008; Hawass *et al.* 2010). The latter study successfully replicated and identified three genes (STVOR, AMA1 and MSP1) specific to *P. falciparum.* Two of these individuals from Hawass *et al's* (2010) study, Tutankhamun (c. 1333-1324 BC) and Yuya (c. 1410-1360 BC), were shown to be carrying multiple malarial infections; while two individuals from Nerlich *et al's* (2008) study displayed severe *Porotic* lesions. It has been tentatively proposed that the osteological lesions identified on Tutankhamun are compatible with those seen in sickle cell disease (Timmann *et al.* 2010); however, further genetic studies are required to determine the presence of a genetic immunity.

These studies provide the earliest evidence for *P. falciparum* and a reliable *terminus ante quem* for the existence of the strain in the Mediterranean region. The evidence, dating to the late fifteenth to fourteenth century BC, is contemporary with the Late Bronze Age of mainland Greece; a chronological period in which trade routes between Egypt, Crete and the Greek mainland were extremely active[13]. Modern malarial studies would suggest that the distribution of the parasite and malarial vectors would have expanded geographically with these developing trade routes (Cline 1994; Lounibos *et al.* 2002; 2007; Tatern *et al.* 2006a,b). It is therefore proposed that the strain, which was clearly active in northern Africa during this period, would have undoubtedly been active in the Aegean, given viable climatic and environmental conditions.

An earlier introduction date for P. falciparum

Attempts to establish the existence of malaria at an earlier juncture of prehistory than the Late Bronze Age have led scholars to consider the origins of the *Plasmodiae* strain. Recent advances into the genetic variability of *P. falciparum* have resulted in highly contradictory theories as to whether the parasite could have been introduced into the Aegean as early as Angel (1966; 1969a; 1971) suggested. Some studies have indicated that the strain evolved in Africa just c. ~5000 to ~10,000 years ago, in conjunction with the adoption of agriculture and increased human population sizes (Rich *et al.* 1998; 2009; Volkman *et al.* 2001). Prior to this event, it is suggested that a less pernicious strain, a 'proto-*P. falciparum*', existed throughout mankind's existence, having diverged from the chimpanzee parasite *P. reichenowi* approximately 5 to 11 million years ago (Coluzzi 1999; Carter *et al.* 2002).

13

Relative phase of the Bronze Age	Relative chronological phase on Greek Mainland	Cal. BC (Manning 1995)
Late Bronze Age	Late Helladic IIIA	1435-1360
	Late Helladic IIIB	1360-1200

Scholars have suggested that the theory of a recent, Neolithic origin would account for the exceptional pathogenicity of the strain, as *P. falciparum* is largely considered incompatible with small or scattered population groups such as those of the early prehistoric period (de Zulueta 1994; Coluzzi 1999; Hume *et al.* 2003). This theory has weaknesses however, as studies of modern hunter-gatherer societies have shown that while there is a substantially higher parasite burden and greater efficiency of transmission within larger, sedentary groups, it is possible for infection to be sustained amongst small, transient population groups. Research has shown that *P. falciparum* can afflict small semi-sedentary or nomadic population groups, with a density as low 100 individuals, sufficiently severely to cause immunities to arise. In these circumstances, the parasite burden is supported by irregular (sometimes highly irregular) contact with other groups through seasonal movements, migration and trade (Fix 1984; de Zulueta 1994; Alves *et al.* 2002; Anosike *et al.* 2004; Galardo *et al.* 2007). The success of the strain therefore depends upon the degree of contact with other communities.

Other aDNA studies have refuted the theory of a recent evolution, indicating that the modern strain of *P. falciparum* emerged c. 100,000 – 200,000 years ago (Carter *et al.* 2002; Hughes *et al.* 2001; 2002; Mu *et al.* 2002; Jongwutiwes *et al.* 2005). This line of evidence has led scholars to suggest that *P. falciparum* is "one of mankind's oldest, deadliest and most persistent foes", having evolved alongside *Homo sapiens sapiens* (Sallares 2002: 27). Some aDNA studies have, however, synthesised these two contradicting theories (figure 1.5), hypothesising that the strain evolved at an early date (c. 200,000-100,000 years ago) and underwent a further expansion c. 10,000-5,000 years ago.

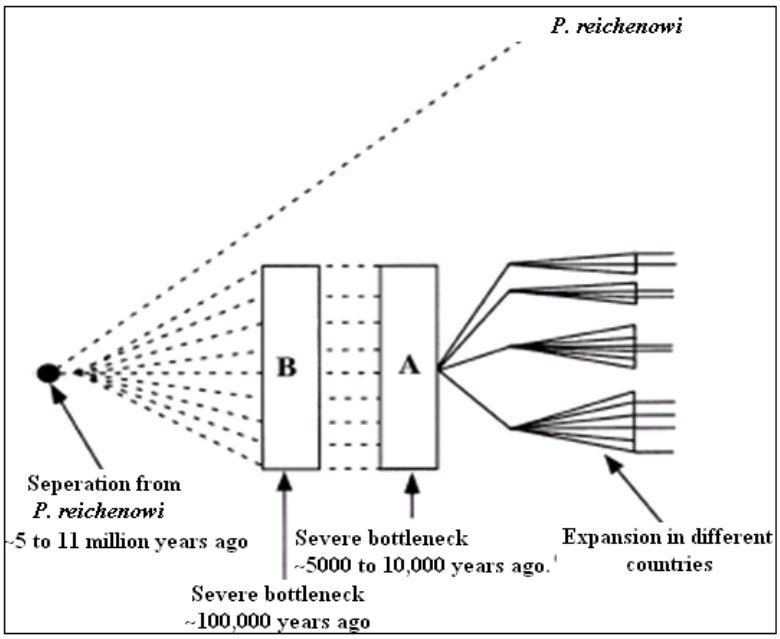


Fig. 1.5: The evolutionary history of *Plasmodium falciparum.* The debate questions the date at which the modern strain occurred; (**A**) suggests a very recent origin occurring c. 5000-10,000 years, (**B**) suggests an earlier divergence. Joy (*et al.* 2003) suggest the differing results reflect separate population expansions *(After* Su et al. 2003: fig. 1: pg. 894).

The divergent results are, therefore, suggested to reflect these different population expansions; this would suggest that different plasmodial populations have different origins and ages due to repeated migrations out of Africa (Conway 2002; Joy *et al.* 2003). This latter theory would suggest that the strain was compatible with smaller human population groups until the Neolithic period, when it underwent a further evolutionary mutation, adapting to sedentary, agricultural communities. It is therefore concluded, based on the latter study, that *Plasmodium falciparum* would have existed in its present form during the Mesolithic period. The disease would, therefore, have undoubtedly been adapted to small host population groups, having evolved alongside mankind (Sallares 2002) and may have migrated out of Africa into the Levant and eastern Mediterranean during the repeated population movements of the late Pleistocene and early Holocene (Semino *et al.* 2000; Templeton 2002; Joy *et al.* 2003; Luis *et al.* 2004). The newly mutated strain of c. 10,000 to 5,000 years ago is suggested to have similarly migrated into the Aegean with subsequent population movements.

The Anopheline vectors

There are, however, further arguments against the presence of malaria in the prehistoric Aegean. Scholars have debated whether the *falciparum* strain could have survived within the Mediterranean at as early a juncture as the Mesolithic due to climatic, environmental and epidemiological factors, which may have mitigated the efficiency of the mosquito vectors (Bruce-Chwatt *et al.* 1980; de Zulueta 1994). The malaria *Plasmodiae* require a mosquito host for the completion of the lifecycle; in the Mediterranean region malaria is transmitted by a single genus: *Anopheles* of the family *Culicidae* in the order *Diptera*, a group which is estimated to date to the Middle Permian (c. 245-237 million years ago) (Blagoderov *et al.* 2002). Of 400 species within this genus only approximately 60 species are considered significant in the transmission of malaria and in each region only three to four species are considered important vectors. Within the Palaearctic region[14] the *Anopheles maculipennis* complex is the most dominant (figure 1.6) (Beljaev 2002); due to the ancient origin of the family, it is assumed that the behaviour and relationship between vector and parasite has not altered significantly since the Mesolithic period (Bruce-Chwatt *et al.* 1980). Modern studies relating to this genus are therefore used as a frame of reference.

Scholars have argued for a later introduction date of *P. falciparum* into the Aegean based on the discovery that infectivity of the mosquito depends on the geographical origin of the parasite and vector (James *et al.* 1932). Early twentieth century studies discovered that many Mediterranean vectors, such as *A. atroparvus, A. hyrcanus* and *A. messae* were largely refractory to foreign or tropical strains of *P. falciparum*, although highly susceptible to the autochthonous strains and to foreign strains of *P. vivax* and *P. malariae* (Shute 1940; Ramsdale *et al.* 1975; Dashkova *et al.* 1982). Based on these discoveries, scholars have

[14] Europe, North Africa, Asia including the Japanese Islands and Arabia including Iraq, Iran and Afghanistan (Bruce-Chwatt 1980: 106)

argued that *P. falciparum* or the vectors (or both) would have had to undergo a long "process of selection" (although the length is unspecified) before the more virulent strain of malaria and the mosquito vectors could adapt, allowing the autochthonous vectors to transmit the strain (Bruce-Chwatt *et al.* 1980: 14).

Epidemiological studies into the history of malaria in Greece further suggested that once the parasite and vector were compatible, the native vectors were not sufficiently virulent in biting habits or sufficiently anthropophilic[15] to support a heavy disease burden amongst a human population. It was therefore suggested that *P. falciparum* could only have been a rare, intermittent disease until the more virulent, primary vectors, such as *A. sacharovi* and *A. superpictus*[16] which would have been adapted to the tropical parasite, were introduced into the Aegean from their suggested original distribution in southern Asia/Africa and the Near East respectively (Bruce-Chwatt *et al.* 1980; de Zulueta 1994).

The refractoriness of the autochthonous *Anopheles* may not, however, have presented as significant a barrier as initially suggested. Firstly, the unspecified 'long' period required for the mutual evolutionary selection and adaption of parasite and vectors would have been available due to its ancient origin (Hughes *et al.* 2001; 2002; Sallares 2002; *et al.* 2004; Mu *et al.* 2003). Secondly, and most significantly, recent studies have noted that the refractoriness of the Mediterranean vectors is not as absolute as first suggested (Eling *et al.* 2003; Sousa *et al.* 2007). Research into the susceptibility of *A. plumbeus* has shown that the vector is highly receptive to foreign strains of *P. falciparum*, while studies from the UK and from Germany indicate that not only is the vector susceptible to the parasite under laboratory

[15] Anthropophilic: favouring human blood over that of animals.
[16] *A. labranchiae* is also a primary vector; however historical malarial records from Greece do not list this as a common species. It is not, therefore, considered within this study (Lividas *et al.* 1941; Sakellariou *et al.* 1977; Kampen *et al.* 2003).

***Anopheles* vectors of Greece**	
Primary Vectors	**Secondary Vectors**
A. maculipennis s.s Meigen, 1818	*A. algeriensis* Theobald, 1903
A. sacharovi Favre,1903 Synonyms: *A. elutus*, Edwards 1921	*A. atroparvus* van Thiel, 1927
A. superpictus Grassi, 1899 (Subgenus Cellia)	*A. claviger* (Meigen, 1804) Synonyms: *A. bifurcatus* Meigen, 1818
	A. plumbeus Stephans, 1828 Synonyms: *A. nigripes* Staeger, 1839
Rare Vectors	
A. hyrcanus (Pallas, 1771) Synonyms: *A. pseudopictus*, Grassi, 1899	*A. melanoon* Hackett, 1934
A . marteri Sevenett und Prunelle, 1927	*A. subalpinus* Hackett and Lewis, 1935

Fig. 1.6. Common vectors of Greece. Following the International Code of Zoological Nomenclature, the surname of the author who first named the species is added without brackets. Where a new name has been given, the author's name is given in brackets (Lividas *et al.* 1941; Sakellariou *et al.* 1977; Bruce-Chwatt 1980; Kampen *et al.* 2003). Primary vectors are indicated in **bold.** s.s: *senso stricto*- indicating a sub-species name rather than the name of the species complex.

conditions but also that it is highly successful at transmitting the disease (Blacklock *et al.* 1920a; Marchant *et al.* 1998; Krüger *et al.* 2001; Eling *et al.* 2003). The prevalence of this sylvan mosquito has decreased in modern and historical periods in Greece due to widespread deforestation and has not therefore been considered as a serious threat during the early twentieth century (Balfour 1936; Peus 1954); however, recent studies in wooded regions of Spain, Portugal and Croatia indicate that this vector is a sporadic contributor to the disease (Merdić *et al.* 2004; Marí *et al.* 2008), while research in Germany, the Netherlands and historical studies from USSR have identified this vector as significant factor in malarial

transmission (Blacklock *et al.* 1920a; Gutsevich *et al.* 1974; Becker 2003; van Bortel *et al.* 2009).

Recent studies have also shown *A. atroparvus* and *A. melanoon* to be susceptible to African strains of *P. falciparum*, although *A. hyrcanus* was found to be refractory (Sousa *et al.* 2007). These latter vectors are not extremely efficient unless in high densities (Jetten *et al.* 1994), however, these studies have highlighted the possibility that refractoriness is not as universal amongst Mediterranean vectors as initially thought and transmission of *P. falciparum* may not therefore have been as delayed as previously suggested. Transmission would not therefore have hinged upon the presence of the tropical *Anopheline* vectors; however the efficiency of transmission would have undoubtedly been increased by these vectors. The date at which the tropical vectors, *A. sacharovi* and *A. superpictus,* could have been introduced into the Aegean therefore remains an important point, although it is not considered as crucial as previously suggested (Bruce-Chwatt *et al.* 1980; de Zulueta 1994).

Angel (1966; 1971) argued that this migration occurred during the Mesolithic period, suggesting that the climatic amelioration following the Last Glacial Maximum created a high malariogenic capacity across the Mediterranean (discussed above). The date of the introduction of the foreign vectors into the Aegean would also, however, depend upon the malariogenic capacity of the environment. Bruce-Chwatt *et al.* (1980) have argued that the Aegean landscape was too heavily forested for the tropical vectors to survive, as *A. sacharovi* and *A. superpictus* favour open landscapes (see chapter two). It was therefore concluded by Bruce-Chwatt *et al.* (1980), and by subsequent scholarly works, that *P. falciparum* could not have been introduced into the Aegean until the large scale deforestation of the Hellenistic or Roman period (third to first century B.C) (Bruce-Chwatt *et al.* 1980; de Zulueta 1978; 1994; Grmek 1994).

This argument is refuted ; firstly, Sallares (2002) has argued that if *P. falciparum* is in fact of an ancient origin, having emerged and dispersed out of Africa c. 100,000 to c. 200,000 years ago, the strain and the tropical vectors would be highly adapted to forested environments, which prevailed across Africa prior to deforestation of the agricultural period. The environment of the Aegean would not therefore have presented a barrier to an early introduction of the tropical vectors. Secondly, it is concluded here that the strain could have been transmitted by the local Aegean vectors, some of which are now known to be susceptible to *P. falciparum* infection (see above) and all of which would have been well adapted to the local landscape. The introduction date of the strain into the Aegean need not therefore entirely depend upon the degree of vegetation cover.

Thirdly, and most significantly, it is proposed here that Bruce-Chwatt (*et al.* 1980) and de Zulueta's (1994) conclusions as to the environmental conditions of the Greek mainland are erroneous. Environmental studies, based on pollen cores and on floral and faunal remains from archaeological excavations, indicate that even the landscapes of the very early Holocene were never entirely forested. Areas of suppressed vegetative growth such as phrygana (lowland dwarf shrubs and herbs), garrigue (open shrub land; often growing on limestone slopes), shiblyak (intermediate deciduous shrub community), maquis (tall evergreen shrub community), meadows, steppe, savanna, open slopes (often due to a lack of soil depth for vegetation) and coastal zones constituted a high proportion of the varied, mountainous landscape of the Aegean (Bottema 1974; 1990; Hansen 1991; Jahns 1993; Grove *et al.* 2003). Continuous dense forestation within the highly diverse topography of mainland Greece has therefore never existed, and the tropical vectors could, therefore, have been supported at an earlier date (Rackham 2008). While malarial transmission is not suggested to have entirely depended upon these tropical vectors, it is acknowledged that their presence would have undoubtedly increased the malarial burden; the capacity of the environment for these vectors

therefore remains an important point and will be considered with regards to the settlements of Franchthi Cave, Nea Nikomedeia and Lerna in chapters four to six.

A synthesis of the existing molecular and epidemiological data therefore suggests that the evidence regarding the presence of *P. falciparum* during the prehistory of the Greek mainland is conflicting. However, a synopsis of recent aDNA, osteological and environmental studies would suggest renewed support for Angel's (1966) theory that *P. falciparum* was present in the Mediterranean during the Mesolithic to Late Bronze Age (Schultz 2001; Mu *et al.* 2002; Joy *et al.* 2003; Hapiot 2003; Stravopodi *et al.* 2009).

The 'lesser' strains

The debate regarding the presence of *P. falciparum* within the Aegean in early prehistory should not, however, overshadow the significance of other malarial strains. While *P. malariae* and *P. vivax* cannot be held responsible for the development of β-thalassemia, both carry a heavy disease burden with strong economic and social repercussions that Price *et al.* (2007) and Baird (2007) consider to have been greatly underestimated in malaria studies (see chapter two). The significance of these strains in prehistoric settings has also largely been overlooked.

P. vivax

The geographical origin of *P. vivax* has been heavily debated; studies regarding the prevalence of RBC Duffy negativity in Africa, which confers immunity against *P. vivax,* have been used to argue for an African origin for the strain (Carter *et al.* 2002). DNA studies have, however, suggested that the strain developed in southern Asia (Escalante *et al.* 2005; Mu *et al.* 2005) and has an ancient origin, with the majority of dates converging between c. 217,000 and c. 314,000 years ago (Feng *et al.* 2003; Jongwutiwes *et al.* 2005). It is considered that the

strain reached Africa and the eastern Mediterranean through the dispersal of *Homo erectus* populations from southern Asia (Jongwutiwes *et al.* 2005; Mu *et al* 2005).

P. vivax is suggested to have been introduced into the Aegean at an earlier date than *P. falciparum,* as the parasite has a far greater tolerance of colder temperatures and is highly adapted to smaller population groups (Hume *et al.* 2003; Carter *et al.* 2003). The strain is firstly extremely transmissible and secondly, the strain remains dormant within the human host; relapses often occur 3-5 years after initial infection (Bruce-Chwatt 1980). This permits the parasite to subsist amongst very sparsely distributed human populations, which are less conducive to *P. falciparum*. The receptivity of the Aegean mosquito vectors to this strain has led to a wide acceptance that *P. vivax* was present in the Aegean during the early Holocene (Blacklock *et al.* 1920a; Shute 1940; 1951; *et al.* 1974; Dashkova 1977; Bruce-Chwatt *et al.* 1980). Most scholars consider that the strains could have been transmitted throughout the warmer phases of the Late Glacial Maximum (Bruce-Chwatt *et al.* 1980; de Zulueta 1994; Carter *et al.* 2002; Hume *et al.* 2003).

P. malariae

P. malariae is also likely to have been introduced into the Mediterranean far earlier than *P. falciparum*. The origin of the strain is suggested to predate the divergence of the human and Great Ape lineage, which occurred approximately 5 million years ago; the migration of the strain out of Africa into the Mediterranean could therefore have occurred at any stage during these five million years (Carter *et al.* 2002; Das *et al.* 2007). Like *P. vivax,* the parasite is suggested to have been able to inhabit the eastern Mediterranean region during the Late Glacial Period, as it is more tolerant to cold conditions. Furthermore, *P. malariae* is arguably ideally suited to low or scattered population densities of both human or vector hosts, more so than *P. vivax* and particularly than *P. falciparum,* as the parasite can lie dormant within the

human host for over 50 years and still remain infectious to mosquitoes (Bruce-Chwatt 1980; Garnham 1966; Carter *et al.* 2002). The long-term nature of the disease can therefore sustain transmission amongst transient groups, although infection rates and the disease burden would be far greater amongst sedentary or semi-sedentary societies (Hume *et al.* 2003). The introduction of these strains into the Aegean would also have been facilitated by the susceptibility of the autochthonous vectors of the Mediterranean region to *P. malariae* (Blacklock *et al.* 1920a; Shute 1940; 1951; *et al.* 1974; Dashkova 1977; de Zulueta 1994).

P. malariae would have been the most efficient parasite amongst dispersed hunter-gatherer groups of the early Holocene and both this strain and *P. vivax* would have increased in prevalence as human population groups increased in number and societies became sedentary. It is therefore concluded that *P. malariae* and *P. vivax* are highly likely to have been present within the Aegean during early prehistory assuming viable climatic and environmental conditions (Bruce-Chwatt *et al.* 1980; Carter *et al.* 2003).

Aims of this thesis

The recent studies into the osteological assemblages of the prehistoric Aegean, the genetic variability of *Plasmodium falciparum* and the susceptibility of *Anopheles* to infection would therefore indicate that the debate surrounding the introduction date for *P. falciparum* and the tropical vectors into the Aegean and Angel's (1966; 1971; 1973) theory of a high but declining malariogenic capacity during the Neolithic and Bronze Age should be re-evaluated. Palaeoclimatic and palaeoenvironmental studies will focus on the three sites of Franchthi Cave, Nea Nikomedeia and Lerna, from which potential indicators of β-thalassemia were identified; this will allow an evaluation of whether the disease, in all three prevalent forms, could have been present and have affected the early populations of the Holocene. This study will attempt to ascertain 1) whether *P. falciparum* malaria could have been introduced at such

an early date as suggested by Angel (1969a; 1971); 2) to determine whether the environment and climate of these sites could have supported all three strains of *Plasmodiae* and 3) whether the climatic and environmental changes between the Mesolithic and Late Bronze Age could have induced fluctuations in the prevalence of malaria as indicated by the proposed changes in the frequency of *Porotic hyperostosis.*

It is noted, however, that the site of Franchthi Cave presents a controversial choice for this study; not only are the osteological remains extremely few for conclusions as to the prevalence of a genetic disorder to be drawn, but a revaluation of the assemblage at Franchthi Cave indicates that Angel (1969a; *et al.* 1986) overestimated the frequencies of anaemic lesions, and concluded that β-thalassemia could not have been the cause (Cook 2000; Stravopodi *et al.* 2009). This thesis will, however, consider the climatic and environmental conditions of Franchthi Cave, as firstly, the chronology of the site allows a closer examination of Angel's (1969; 1971) original theory of a high malariogenic capacity of both the climate and environment from the Mesolithic to the Late Bronze Age. Secondly, if this theory is found to be correct the absence of β-thalassemia does not preclude the possibility that malaria afflicted these early populations any more than the presence of the condition proves the strains existence at that time. It could merely indicate that exposure was insufficient to cause a genetic adaptation. Thirdly, it is proposed here that environmental and climatic reconstructions may help to determine the capacity for the survival of the less virulent strains, *P. vivax* and *P. malariae* during this early period. The site of Franchthi Cave therefore provides an ideal opportunity to test Angel's overall theory and to consider the 'lesser' malaria strains, whose role in potential disease burdens in prehistory have been largely ignored. Firstly, however, the epidemiology and the socio-economic significance of malaria will be considered.

Chapter Two:

Malaria and the *Anopheline* Vectors of Greece

All *Plasmodiae* are characterised by a biphasic growth cycle involving a phase within the mosquito, known as the sporogonic cycle and another phase within the human host, known as schizogony. The parasite begins its life cycle within the female mosquito where it is transmitted to humans through the saliva glands as the mosquito feeds upon the human host (figure 2.1). Once the human has been bitten the parasites move rapidly through the bloodstream to the liver where they invade hepatocytes and multiply; this stage is known as hepatic (or pre-erythrocytic) schizogony. After twelve days to four weeks, the hepatocytes mature into schizonts, which burst, releasing thousands of young parasites known as merozoites into the bloodstream (Bruce-Chwatt 1980).

In the case of *P. vivax,* some schizonts remain within the liver as hypnozoites, these lie dormant within the human host for weeks or even years; *P. malariae* also persists in the human body for extended periods during the blood phase of the cycle (Price *et al.* 2007; Collins *et al.* 2009). During the erythrocytic phase, the merozoites invade red blood cells (RBCs) where the parasites develop into two forms. In an asexual cycle the developing parasites form schizonts in the RBCs, which rupture and release a further batch of merozoites, which invade new RBCs and the cycle continues until slowed or ended by the immune response of the host. A sexual cycle produces male and female gametocytes, which circulate in the blood and are taken up by a female mosquito when taking a blood meal.

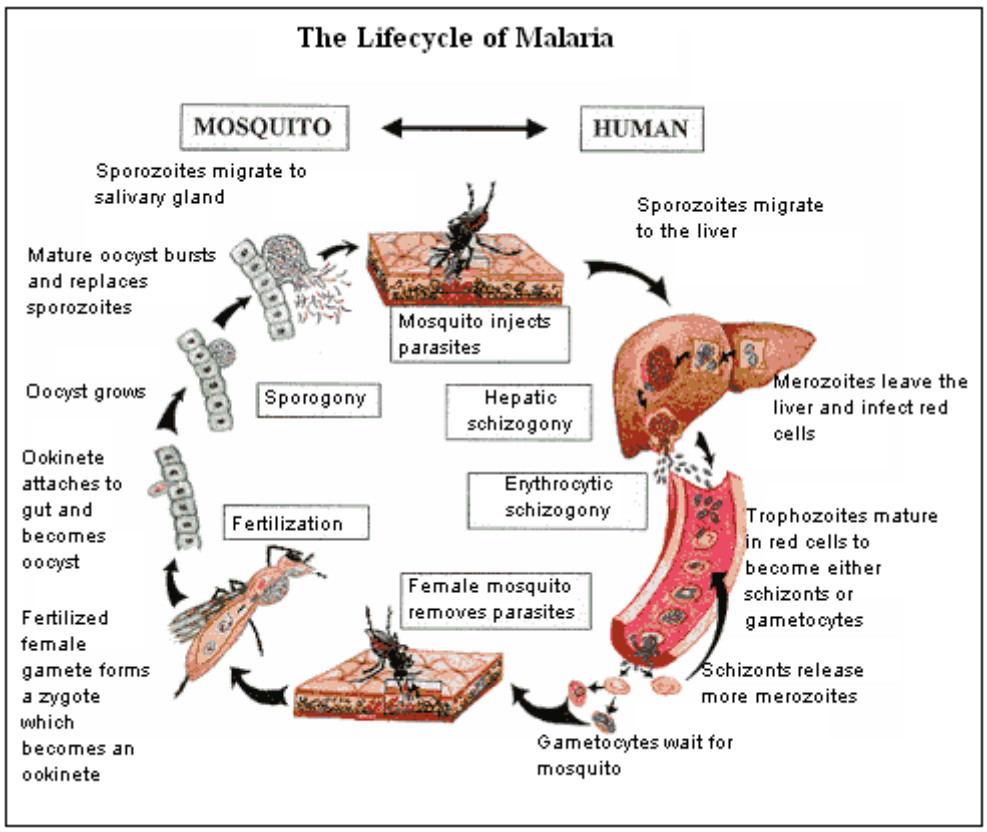


Fig. 2.1: Lifecycle of *Plasmodiae falciparum* (WHO/EMRO 2010)

Within the mosquito, the gametocytes reproduce to form oökinete, which invade the wall of the stomach to form an oöcyst; the rate at which these develop depends upon the external temperature and this is a particularly important factor with regards to the intensity of transmission. On maturing, the oöcysts burst, releasing several hundred sporozoites, which move to the salivary glands. These are then ready to be injected into a human host when the mosquito next takes a meal (Bates 1970). It is worth noting that the malaria parasites are considered to be harmful to the *Anopheles* vectors; there is some evidence to suggest that infection can shorten the survival rate of the mosquito, limiting the population density of the vector and the transmission of the disease (Ferguson *et al.* 2002).

The bursting of the RBCs at the end of the erythrocytic phase results in the onset of fever and other symptoms of the disease, the periodicities of this event varying in the different *Plasmodium* strains and define the particular strain (figure 2.2) (Bruce-Chwatt 1980).

***Plasmodium* species**	**Fever Periodicity**	**Common name**
Plasmodium falciparum	Indistinct	Malignant tertian, Subtertian, Aestivo-autumnal, Tropical, Pernicious
Plasmodium vivax	48 hours	Benign tertian
Plasmodium malariae	72 hours	Quartan Fever

Fig. 2.2: Fever periodicity of the parasites of the Mediterranean (*After* Bruce-Chwatt 1980).

Plasmodium falciparum

This strain is the most virulent of the four species of human malaria, causing 95% of all malaria related deaths (Knell 1991). Its incubation period[17] is shorter than other strains of malaria, lasting between nine days to two weeks. The fever is high and intermittent; reaching up to 41˚C. Infection begins with headaches, prostration, chills, nausea, vomiting and diarrhoea; this stage develops quickly, causing an increasing severity of symptoms (Knell 1991). The parasite causes massive destruction of red blood cells; whereas *P. vivax* and *P. malariae* favour young and old RCBs respectively, *P. falciparum* will attack RBCs indiscriminately, resulting in the infection of c. 10%-30% of all cells (Bruce-Chwatt 1980). Both infected and healthy RCBs are destroyed within the spleen, causing severe enlargement. This progressive loss of blood will cause dangerous levels of anaemia, the enlargement of the

[17]The incubation period is defined by the period between initial infection and the first appearance of the clinical symptoms of the disease (Bruce-Chwatt 1980).

liver, anoxia of various organs[18], stupor and fits; other complications include cardiac arrhythmias, pulmonary insufficiency, and kidney damage leading to renal failure (Bruce-Chwatt 1980). Malarial cachexia is also frequent; a metabolic syndrome characterised by loss of muscle and potentially loss of fat mass, causing weight loss in adults and growth failure in children. The condition can result in a weakening of the immune system, lethargy and depression (Evans et al. 2008).

If the disease is survived or if immunity protects the individual against the severe symptoms, the milder symptoms of *P. falciparum* infection can last for 1-2 years (Bruce-Chwatt 1980). In the absence of immunity, cerebral malaria can begin after the initial symptoms; this occurs when infected RBCs block the capillaries in the central nervous system, causing acute delirium, meningitis, epilepsy and severe mental impairment. The mortality rate of this condition is extremely high (Bruce-Chwatt 1980; Nájera *et al.* 1996).

Plasmodium vivax

P. vivax is the second most common malarial strain in the modern world, affecting over 75 million people each year (WHO 2009). A genetic immunity to *P. vivax,* termed Duffy negativity, is extremely widespread in Africa, affecting 95% of West and Central African populations; however, the absence of this immunity amongst other global populations, including the Mediterranean, is not as yet understood (Carter *et al.* 2002).

The strain has similar clinical symptoms to *P. falciparum,* although the strain is limited by lower parasitaemia due to its selective preference for young RBCs. The incubation period lasts for ten to seventeen days; paroxysmal fevers, reaching up to 40.5˚C, last from two to six hours and return every third day, and are considered more severe than those of *P. falciparum.* The attack causes chills, severe shaking, intense sweating, vomiting and diarrhoea; anaemia

[18] An absence of oxygen, potentially resulting in organ or multi-organ failure.

and often jaundice are common pathological consequences of the disease. Splenomegaly develops and ruptured spleens can cause death, although this is rare (Bruce-Chwatt 1980; Baird *et al.* 2007; Price *et al.* 2007).

Although *P. vivax* infections have historically been seen as less severe than *P. falciparum*, recent studies suggest that the effects of *P. vivax* infections have been underestimated (Baird *et al.* 2007; Price *et al.* 2007). Studies have noted that renal failure, liver disfunction, acute respiratory distress syndrome, cerebral malaria and coma can accompany vivax infection. It has been further noted that when combined in synergistic interactions with other diseases or with severe malnutrition, *P. vivax* may well have a lethal effect (Kochar *et al.* 2005; Baird 2007; Kumar *et al.* 2007; Price *et al.* 2007). The duration of untreated *P. vivax* infection can extend to 3-4 years; the prolonged nature of the disease is caused by repeated, debilitating relapses, which occur due to the reactivation of the dormant hypnozoites which are particular to *P. vivax*. This causes the symptoms to re-emerge long after the initial infection; the patient remains symptomless after the primary attack for some months, when a series of relapses occur 30 to 40 weeks after initial infection. The ability to relapse causes *P. vivax* to be extremely resilient to eradication from either the human host or the environment (Bruce-Chwatt 1980; Imwong *et al.* 2007; Price *et al.* 2009).

Recent studies suggest that the risk of *P. vivax* infection may be greater for individuals that are heterozygous for β-thalassemia; *P. vivax* predominantly favours young red blood vessels and the constant and rapid renewal of RBCs caused by the genetic immunity may therefore increase susceptibility to infection (Premawardhena *et al.* 2008). More studies into the relationship between β-thalassemia and *P. vivax* are required; however, studies have noted a mild increase in vivax infection in α-thalassemia sufferers (Williams *et al.* 1996). If this is the case, and if Angel's theory that the osteological lesions represent β-thalassemia is correct, *P.*

vivax may have presented a greater threat to the early populations of Greece than suggested by earlier studies.

Plasmodium malariae

Quartan malaria, spread by *P. malariae*, is a milder strain whose incubation period can be as much as six weeks. The fevers, occurring every fourth day, reach up to 40°C. The clinical features of this strain are largely similar to *P. falciparum* and *P. vivax* although significantly milder; anaemia and other complications are less pronounced although rigors and splenomegaly are often severe. Infection can also cause abortion and premature birth (Rogerson *et al.* 2007). *P. malariae* is not particularly virulent as the percentage of infected RBCs rarely exceeds 1%; mortality rates are consequently lower and only occur in synergistic interaction with existing conditions, such as respiratory diseases. The infection is however particularly persistent, causing asymptomatic infections which can last for decades. Relapses can occur 50 years after the initial infection, which permits the strain to persist within scattered populations and resist eradication from either humans or from the environment (Bruce-Chwatt 1980; Collins *et al.* 2009).

Mixed Infections

Infections of more than one malarial strain in both human and mosquito vectors are extremely common, even in areas of low transmission. The susceptibility of the vectors varies from species to species; studies into the capability of all the Mediterranean vectors are extremely limited, however, it is noted that *A. sacharovi* is capable of carrying both *P. falciparum* and *P. vivax* simultaneously, while *A. atroparvus* can be infected by all three parasites (Mckenzie 1997).

Malaria studies in southern Greece between 1930 and 1933 noted a high prevalence of mixed infections within the human host; 85% of 107 individuals showed infection of one species and 45% were suffering from mixed infections, predominantly of *P. falciparum* and *P. vivax* although all three *Plasmodiae* were not uncommon (Balfour 1935). It was proposed that mixed infections affected a large percentage of populations in moderately or highly endemic regions in Greece, which included both the Peloponnese and Greek Macedonia (Balfour 1935; Lividas *et al.* 1941). Concurrent infections within the human host appear to interact with important effects on host immunity; however, the mechanisms of this are still only partially understood. Parasites appear to engage in mutual suppression, with one species predominating; this dominance leads to a great underestimation of the frequency of mixed infections in endemic regions (Luxemburger *et al.* 1997; Mayxay *et al.* 2004). Recent studies have shown that a mixed infection of both *P. falciparum* and *P. vivax* can reduce the risk of severe malaria four-fold, resulting in a lower risk of severe complications (Desai *et al.* 2007). Other studies have however noted that the peaks of parasitaemia of the various plasmodia can occur sequentially, leading to a higher degree of debilitation (Mayxay *et al.* 2004). The combination of infections can also boost the efficiency of the life cycle of the various *Plasmodiae*; the effectiveness of the reproductive cycles of *P. falciparum* appears to increase when combined with *P. malariae* infections (McKenzie *et al.* 2002). The effects of mixed infection therefore appear to vary considerably, and the outcome of such combined parasitic burdens is hard to predict. It is evident, however, that it is extremely common for populations in endemic regions to harbour more than one *Plasmodiae*.

Transmission and malaria infection

The degree to which a population is affected by these parasites depends on the level of exposure to the disease. There are two general categories pertaining to the incidence of malaria: *endemic* and *epidemic*. The term endemic refers to a constant incidence of the disease within a given area; endemicity may, however, vary from region to region and the term is therefore sub-categorised and defined by the density of vector populations and the frequency of infectious mosquito bites per person per unit of time (figure 2.3) (Macdonald 1957).

Classification		**Definition**
Stable Malaria	Holoendemicity	Intense perennial transmission. High degree of immunity amongst local populations. Epidemics uncommon.
	Hyperendemicity	Intense, seasonal transmission; immunity amongst local populations high but variable. Epidemics possible.
Unstable Malaria	Hypoendemicity	Little transmission and disease burden is negligible. Frequency of immunity varies. Epidemics possible.
	Mesoendemicity	Low transmission rates. Immunity varies. Epidemics possible.

Fig. 2.3: Classification of Endemic Malaria

High transmission rates, found within stable endemic regions, can result in the development of genetic immunities amongst the indigenous populations (Bridges *et al.* 2008). Populations within endemic regions, both stable and unstable, can also develop acquired immunity, known as premunition, through repeated exposure to the parasite; the condition is highly

prevalent in regions of stable transmission and more variable in regions of unstable disease patterns (Macdonald 1957). Premunition or 'partial immunity' protects the individual against the severe symptoms of malaria, although a high parasitic burden will persist (asymptomatic parasitaemia). The mechanism of this form of immunity is not well understood; it is unclear whether immunity develops as a result of multiple previous infections or whether protection is caused by the presence of parasites within the blood stream. Recent studies tend to support the latter theory (Doolan *et al.* 2009).

Premunition, while highly beneficial, is limited in its capacity; firstly, the protection is short-lived. A short hiatus in transmission can cause a population to become vulnerable to infection when transmission resumes (Thomson 1933). This occurs within hyperendemic regions, such as proliferated in lowland areas of Greece before the eventual eradication of the disease, particularly in the Peloponnese and Greek Macedonia, as well as under meso- and hypoendemic regions (Balfour 1935; 1936; Macdonald 1957; Stamatoyannopoulos *et al.* 1966; Bruce-Chwatt 1980). Secondly, premunition is both *strain-specific* and *clone specific*; immunity against one strain does not, therefore, confer protection against another plasmodial strain. A single strain can furthermore show multiple mutations, indicating that an individual who has developed immunity to a *Plasmodiae* strain will not be protected from the same *Plasmodiae* from another region (Babiker *et al.* 1997; Freitas-Junior *et al.* 2000). Population movements or migrations can therefore increase the risk of infection for those lacking genetic immunity (Prothero 1977).

In highly endemic regions, protection can begin at infancy due to a trans-placental transfer of protective antibodies to the foetus; known as congenital immunity, this provides newborns with immunity against infection until about six months of age. Infants are therefore often spared the clinical severity of malaria infection but will suffer from severe and debilitating anaemia. In the absence of congenital immunity, premunition against *P. vivax* will develop

by the age of 10-15 after repeated infections, resulting in the suppression of the severe clinical symptoms of the disease; infants and young children are therefore at the greatest risk of infection (Baird *et al.* 2007). In *P. malariae* premunition develops at an earlier age although the typical age is unspecified (Collins *et al.* 2007). In the case of *P. falciparum,* the risk of disease increases until the age of two to five years, by which time the frequency of exposure to malaria generally leads either to death through severe malarial infection (cerebral malaria is common amongst young children) or to the development of acquired immunity (Rogerson *et al.* 2007; Doolan *et al.* 2009). The risk of disease decreases after the age of 5 and adults rarely carry high parasitic burdens, but when they do succumb to illness through a lapse in immunity, the symptoms are often extremely severe (Doolan *et al.* 2009).

The probability of *P. falciparum* related mortality in endemic regions is calculated to be approximately 2-3% due to the acquisition of immunity; however while the threat of the severe clinical symptoms of malaria is negligible, the individual is burdened by anaemia, malnutrition and malarial cachexia. These complications, particularly severe anaemia, are extremely common and present a distinct danger, especially to children (Doolan *et al.* 2009). The most vulnerable individuals within endemic regions are therefore young children aged between one and five years that have yet to develop acquired immunity and the elderly, whose immune systems place them at increased risk. However, pregnant women are considered a particularly vulnerable group, as natural defence mechanisms are severely reduced during pregnancy (Desai *et al.* 2007; Rogerson *et al.* 2007). *P. falciparum* can cause infection of the placenta, potentially causing prematurity, low birth weight, anaemia or miscarriage. Stillbirths and miscarriage are rarely associated with *P. vivax* or *P. malariae;* congenital malaria is, however, an equal risk as with *P. falciparum* infections (Mendis *et al.* 2001). Pregnancy can also awaken any latent infection within the mother, augmenting the risk to both the mother and the unborn child (Bruce-Chwatt 1980; Desai *et al.* 2007).

Epidemic malaria refers to a sharp rise in the incidence of malaria; these are precipitated by 1) an increase in the efficiency or population density of *Anopheles* vectors, 2) increased contact between humans and vectors and 3) the augmented susceptibility of the human population, for example, due to migrations or due to lowered immune systems (figure 2.4) (Russell 1952). Epidemics of *P. falciparum* are considered to be "among the most lethal forces of nature" (Carter *et al.* 2000: 567), as the incidence of severe complications, including cerebral malaria, congenital malaria and other severe complications is exceptionally high and mortality rates are estimated to be ten times higher than those of endemic areas (Bruce-Chwatt 1980; Kiszewski *et al.* 2004). *P. malariae* and *P. vivax* epidemics result in high morbidity rates amongst all age groups and *P. vivax* may result in a death toll, however the mortality rates are not as high as those of *P. falciparum* (Mendis *et al.* 2001; Baird 2007).

Epidemics occurring within endemic regions will result in increased morbidity rates which frequently result in a high percentage of a population to be incapacitated at some interval, although the prevalence of genetic immunities or the maintenance of premunition will limit the burden (Balfour 1936; Lividas *et al.* 1941; 1946; Bruce-Chwatt 1980). Epidemics within non-endemic regions are, however, exceptionally damaging as populations will lack immunities due to irregularity or brevity of exposure. All age groups within the exposed population will therefore be highly vulnerable to infection.

Amongst the non-immune, infection during pregnancy can potentially result in the transfer of a malarial infection to the unborn child through inter-uterine transmission of malaria; this condition, known as congenital malaria, occurs in all strains of malaria. Infection of the placenta can furthermore prevent the transfer of antibodies from the mother to the child, increasing the infant's vulnerability to other diseases (Mendis *et al.* 2001; Rogerson *et al.* 2007; Desai *et al.* 2007).

Classification	Definition
Long- term	Extremely prolonged although interrupted by numerous recessions. Can show 20 year periodicity although some wholly irregular. Caused by highly favourable conditions.
Periodic	Regular cyclical changes to endemic malaria, caused by seasonal variations in climate. Occurs annually in sub-tropical and temperate regions with the aestivo-autumnal outbreak of *P. falciparum.*
Irregular	Occurs due to an event facilitating transmission above normal levels. Migration, social disruption, extreme weather events or the introduction of a new vector are common causes.

Fig. 2.4: Classification of Epidemic Transmission

Epidemics can be initiated through climatic and environmental factors and by changes in human behaviour. Increased population mobility is a particularly significant factor (McNeill 1979; Prothero 2001). Migrations, especially seasonal population movements such as temporary labourers, can result in regular and severe epidemics if non-immune individuals are introduced into a region with a high malariogenic capacity, or if a new parasite is introduced into an area. The clone-specific nature of acquired immunity can furthermore render a population vulnerable to strains that have developed within another region (Babiker *et al.* 1997; Freitas-Junior *et al.* 2000). Large scale immigrations, occurring due to environmental deterioration, economic necessity, conflicts and natural disasters, can cause long-term disruption to established disease patterns. The effects of such outbreaks are far reaching, affecting the efficiency of health systems, economic and social structures (Bruce-Chwatt 1980; Prothero 2001). Malaria can also, however, be precipitated through the changes the new population group effect upon the environment and through the technologies they introduce. New agricultural techniques, crops, building methods or social activities can alter

human and vector behaviour, potentially increasing contact between the mosquito and human host (Martens *et al.* 2000).

Social and economic effects of malaria

It has been noted that where malaria prospers most, societies prosper least (Sachs *et al.* 2002). Mortality rates cause a heavy toll on demographics as high rates of infant mortality limit the fecundity and therefore the size of the population. However, the consequences of malaria extend far beyond the immediate clinical manifestations of the disease; more severe complications include blindness and loss of hearing and loss of motor function (Sachs *et al.* 2002; Fernando *et al.* 2003; Clarke *et al.* 2008). Cerebral malaria can cause long term brain damage in older children or adults; young children can recover brain functions although such a recovery is not absolute. Language skills are often severely affected (Carter *et al.* 2006). It is assumed however that individuals are unlikely to survive cerebral malaria in the absence of medical intervention, and the survival rate in prehistoric societies is therefore debateable (Holding *et al.* 2001).

Morbidity rates, however, carry an equally severe cost with regards to social and economic progress (Breman 2001). Repeated infections can result in various psychological and mental complications, including depression, reduced concentration levels, poor initiative and impaired intellectual functioning (Fernando *et al.* 2003; Olney *et al.* 2007). Lower birth weights, caused by maternal infection and malnutrition can also cause cognitive problems in later stages of development, while disrupted development rates in children will result in weaker adults. Mental complications are widespread within areas of moderate to high endemicity where malaria cachexia is common. Jones (1909), rather unsympathetically, remarked upon “vacillation, indecision [and] cowardly depression” amongst sufferers

(1909:105), while MacCulloch (1827) noted that in their "languor [victims] make no exertions to better their condition" (1827: 433).

There is also some evidence to suggest that iron-deficiency anaemia, a condition which accompanies genetic immunities such as β-thalassemia, can also cause lethargy, slower development times, lower concentration and impaired motor activity amongst young children (Olney *et al.* 2007). Anaemia will also reduce an individual's capacity for work, affecting stamina, strength and aerobic ability even in physically undemanding tasks (Bridges *et al.* 2008). The lethargy, mental and physical exhaustion associated with the disease, malarial cachexia and anaemia, are strong contributing factors in low social, cultural and economic productivity (Bruce-Chwatt 1980; Mendis *et al.* 2001; Sachs *et al.* 2002).

Endemic regions therefore carry a heavy disease burden; recurrent infections with any species of malaria parasite are eventually so debilitating that life expectancy can be reduced to half that of populations that live within regions that are unaffected by malaria. The effects are such that local populations tend to become "aged even in childhood [...and their...] brief life [...is...] but one disease" (MacCulloch 1827: 7). During the late nineteenth to early twentieth century, the high endemicity of malaria in Greece constituted "one of the most important causes of economic misfortunes, engendering poverty [and] ruining the quality of the race"[19]. The disease limited productivity, as repeat infections and relapses incapacitated individuals both physically and mentally at irregular intervals, causing 3-6 days of debility with each infection (Balfour 1936; Lividas *et al.* 1963; Greenwood *et al.* 2005). The disease can therefore result in a considerable loss of man hours; the acute cases, lingering complications of the disease and time spent caring for the sick, limits the efficiency of the labouring force and reduces hours of schooling.

[19] Ronald Ross: Appeal made to the Greek Government by the Greek Anti-Malaria League 1907, cited in W.H.Jones 1909: 110.

Agricultural and subsistence societies are particularly vulnerable to the relapses and debilitating complications of malaria in endemic regions, as agricultural land is not only conducive for many of the *Anopheline* vectors but their life-cycles also coincide closely with agricultural cycles. In Mediterranean regions, *P. vivax* emerges in mid-spring although relapses frequently occur during late winter and early spring, while *P. falciparum,* otherwise known as the aestivo-autumnal fever, and *P. malariae* emerge in late summer and persist into late autumn/early winter, potentially resulting in epidemics in regions where an endemic-epidemic cycle predominates (Balfour 1935; 1936). The lifecycle of the *Plasmodiae* therefore corresponds to annual agricultural phases of land tillage and of the sowing and harvesting of crops.

Malarial studies from Greece between 1909 and 1960 show that agricultural productivity was severely compromised by these virulent malarial patterns; 75% of 1½ - 2 million cases of malaria per annum affected individuals of a productive age, causing at least 6 sick days per year. Infections were noted to cause 50% to 100% of land workers to be incapacitated during the harvesting period; the disease was therefore seen as a determining factor in agricultural production, leading to the neglect of harvests, reduced yields and potentially to food shortages and malnutrition (Lividas *et al.* 1963; Kontogiorgi 2006). Malaria limited not only productivity but also economic expansion; as populations avoided the regions of high malariogenic capacity, only a small fraction of the total available fertile land was cultivated, thereby limiting the potential agricultural output (Lividas *et al.* 1963).

Studies show that societies afflicted by such repetitive disease patterns develop adaptive strategies to cope with the burden; crops can be replaced with species where the harvest corresponds with a non-malarious season. In some cases this has caused crops with lower nutritional values to be favoured, which can again exacerbate malnutrition (Conly 1975). Transhumance is practiced in pastoral societies, where shepherds and livestock herders move

their flocks to the higher elevations during the spring and summer months, thereby avoiding the height of the malarial season along the valleys and plains. This was a particularly common practice in northern Greece along the malarious Chrysoupolis plain during the early twentieth century; the practice resulted in low to non-existent parasite burdens amongst the shepherds and pastoralists, while the parasitaemia levels of the villagers who remained on the plain were exceptionally high (Barber *et al.* 1936). This would limit the potential damage of the malaria burden to the demographics and economic productivity of a small population.

Malaria can also affect intra-regional or international relations. The potential for infection can strongly suppress trade, particularly between malarious and non-malarious regions, which can cause severe economic damage in incipient societies. The prevalence of endemic malaria in southern Europe during the mid-twentieth century caused Greece, Spain and Portugal in particular to be isolated from common trading markets; a process of economic development only began once the disease was eliminated during the latter half of the century (Sachs *et al.* 2002). The threat not only lies in immediate infection, but also in the geographical expansion of malaria parasites; new strains of *Plasmodiae* can be introduced into a region through both local and extended trading networks, potentially resulting in autochthonous malaria if the local vectors are susceptible to infection from the newly introduced strain. This has repeatedly occurred within Europe in recent years, where multiple cases of *P. falciparum* have emerged due to imported malaria; the particular threat lying not in the individual cases, but in the potential for sustainable transmission patterns (Merchant *et al.* 1998; Krüger *et al.* 2001; Lounibos 2002; Tatern *et al.* 2006b).

Vector species can also expand geographically through population movements and trade routes. Recent studies have shown that *Anopheles* larvae and adult vectors are highly tolerant of extreme environments, being able to travel considerable distances under highly stressful and unfavourable conditions. This permits vectors to survive long and arduous travels

overland, by sea and, in more recent years, by air (Russell 1987). Adult *Anopheles* have been found capable of surviving in the wheels at the exterior of aircraft, enduring temperatures of -52 ˚C for prolonged periods; survival on cargo ships or on overland caravans is therefore comparatively simple. Larvae can be transported within containers or cabin spaces, while adults will rest within cracks or crevasses in fabric and organic materials (Wilson 1997; Lounibos 2007). This can result in competitive displacement, where a foreign vector successfully adapts to the local environment. Climatic and environmental conditions are the greatest barrier to this; invasions of exotic vector species into Europe, for example, have been restricted as they do not hibernate and cannot, therefore, survive the colder climate (Krüger *et al.* 2001: Tatern *et al.* 2006b). In warmer regions however, competitive displacement is a particular threat if the foreign species is more competitive, more receptive to the malaria parasites, or better suited to local habitats than the local vectors. The vector could then become established within the new environment, causing an increase in infection rates (Lounibos 2002; 2007).

Early prehistoric populations are suggested to have been highly vulnerable to malaria. The extensive clinical complications associated with the disease, amongst both the immune and non-immune, would not only have endangered an individual's life and development, but would also have presented severe obstacles to the community. As early subsistence societies relied entirely on labouring capacity, the debilitation of the labourers would risk food production; combined with limited food storage facilities and restricted health care, it is suggested that these societies would be extremely vulnerable to both the acute symptoms of the disease and to the economic and social effects of the disease. Later societies, such as those of the Bronze Age, may have been economically suppressed by such a condition, limiting the potential for trade, international contacts and cultural expansion. The potential effects of malaria on prehistoric cultures should not, therefore, be underestimated.

The climatic and environmental determinants of malaria

In order that the malariogenic capacity of past environments may be reconstructed, the available empirical evidence concerning the main determinants of malaria must be considered. The greatest determinants are climate, environment and vector behaviour; these factors will regulate the success of the disease, establishing population density, efficiency, virulence and the distribution of the *Anopheline* species. As the success of the *Plasmodiae* spp. depends entirely upon the success of its vector host, the viability of the climate and environment for the vectors are crucial to the successful completion of the first stage of the *Plasmodiae* lifecycle. *Anopheles* behavioural traits will, however, determine the second phase of the lifecycle and the nature of transmission. An understanding of the relationship between these factors is therefore essential in attempting a reconstruction of the malariogenic capacity of ancient landscapes.

Climate and malaria

The malarial Plasmodiae

The malarial parasites and the various *Anopheline* hosts are poikilothermic; the development rate of the *Plasmodiae* within the vector (sporogonic cycle), and the reproduction cycle (gonotrophic cycle), abundance, lifespan, digestive rates and biting rates of the vector mosquitoes are all governed by temperature and humidity, and are all factors which dictate the prevalence of malaria in a given area (Gillett 1974; MacDonald 1957). The successful development of the *Plasmodiae* within the vector depends entirely upon temperature; *P. vivax* and *P. malariae* require a minimum of 15-16 ˚C in order to complete the sporogonic cycle, while *P. falciparum* requires a minimum of 18 ˚C-19 ˚C. The risk of transmission is not considered significant until three or four degrees higher than the minimum temperature has been attained; at a constant minimum temperature the development cycle of all *Plasmodiae*

species will last approximately 32-35 days (figure 2.5) (MacDonald 1957; Garnham 1964; Bruce-Chwatt *et al.* 1980).

Increases in temperature and humidity result in increasingly rapid development of the *Plasmodiae* within its host; the shortest development time occurring at 27-31 ˚C. The sporogonic cycle is halted when temperatures exceed c. 35 ˚C or drop below the minimum temperature tolerated by the strain (Boyd 1949; Garnham 1964; Bruce-Chwatt 1980; Martin *et al.* 1995).

	15-16 ˚C	**20 ˚C**	**24 ˚C**	**30 ˚C**
P. vivax	32-35 days	16 days	9 days	7 days
P. falciparum	N/A	20 days	11 days	9 days
P. malariae	32-35 days	30 days	21 days	15 days

.

Fig. 2.5: Temperature and development times of the malarial *Plasmodiae*

The optimum humidity level for the successful completion of the sporogonic cycle is approximately 60%, below which the success of the mosquito host decreases and the parasite will die (Garnham 1964). Humidity levels above 60% simply increase the life span of the adult mosquito, a factor which has been noted as a major cause of epidemics, especially when in conjunction with favourable temperatures (Bruce-Chwatt 1980).

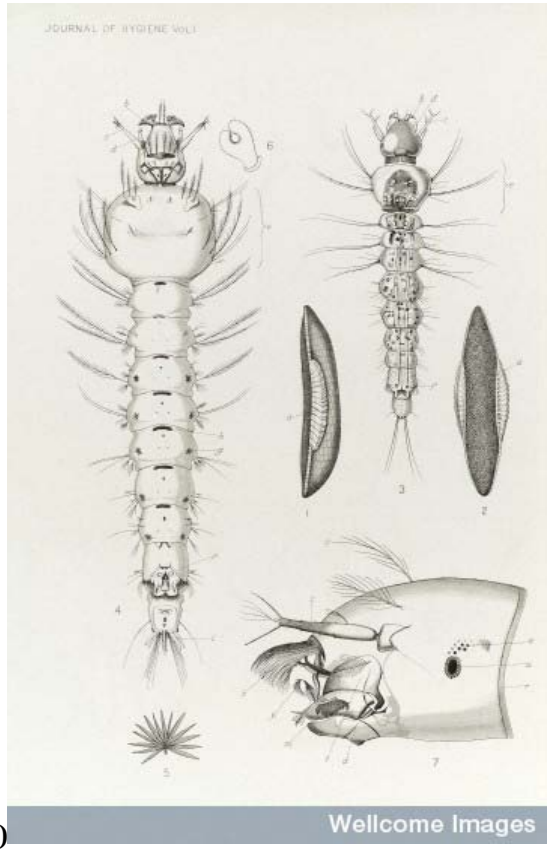
The Anopheline vectors

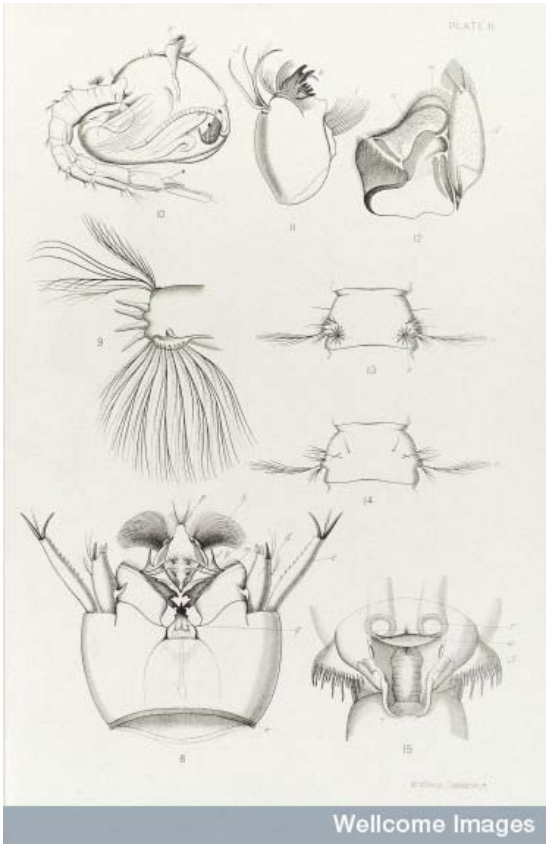
Discerning the climatic tolerances of the *Anopheline* mosquitoes is more complex than those of the *Plasmodiae*; firstly, vectors all have varying climatic requirements and secondly, each has varied behavioural traits, which can expose and protect them from different climatic

conditions. All species, however, are governed by temperature and humidity; the optimum temperatures for the female *Anopheles* are between 25-35 ˚C, while humidity levels of 60% or above are favourable. Under conditions at the lower end of this spectrum, the average lifespan of a female is approximately ten to fourteen days, during which time between eight hundred and one thousand eggs will have been laid (Goma 1966; Bates 1970). Given warmer and more humid conditions the female will survive up to three to four weeks, increasing the frequency of feeding and oviposition; this will result in a larger mosquito population density and potentially in higher infection rates (Bruce-Chwatt 1980; Becker 2003).

Temperature increases will also cause acceleration in the development rates of the aquatic stages of the *Anopheles* mosquito: the eggs, pupae and larvae (figure 2.6). *Anopheline* mosquitoes lay single eggs upon the surface of a water body; once hatched the *Anopheline* passes through four larval stages before developing into pupae and emerging as an adult. The cycle from egg to the adult can take from twenty days at 20˚C, but only seven days at 31 ˚C; even small temperature fluctuations of 0.5-1 ˚C can result in more rapid development rates in the immature stages of the mosquito than constant temperatures can produce. Studies have shown that half a degree increase in temperature can result in a disproportionate increase in vector populations, causing anything from a 30% to 60% rise in population density (Pascual *et al.* 2006). The risk of infection will therefore be augmented.

These increased reproductive and development rates carry further risks for the human population; the rapid development of the eggs, pupae and larvae encourage the creation of far smaller adult mosquitoes, the females of which take a greater number of blood meals, again increasing the risk of transmission. These smaller and hungrier adults are however less fertile, limiting the potential for exponential population expansions (Clements 1963).

a) 

b) 

c) 

Fig. 2.6. The lifecycle and anatomy of the *Anopheline* mosquito: a) the aquatic stages: lateral view of *Anopheline* egg, and the first and fourth instar of the Larval stage. b) Adult *Anopheline* vector (*A. maculipennis*) c) Anatomy of the pupae (Wellcome Library, London)

The behaviour of the mosquito is also regulated by climatic conditions; feeding patterns and the gonotrophic cycle (the cycle from ingestion of the blood to oviposition) are directly affected by temperature and humidity. The rate of blood digestion is increased by hotter, more humid weather, which encourages the *Anopheles* to bite more frequently; this increases the frequency of sporogony, the population density of the *Anopheline* vectors and the risk of infection (Clements 1963; Bruce-Chwatt 1980; Lindsay *et al.* 1996a). Biting behaviour is also determined by microclimatic factors, most specifically by temperature and light. Vectors are sensitive to strong light and midday heat, both of which cause vectors to rest within shaded areas. Most *Anopheline* vectors are therefore crepuscular and biting activity peaks at dawn and dusk when light and temperatures are more suited to vector activity (Shannon 1935; Becker 2003).

Anopheline tolerances to climatic conditions are however narrow; unfavourable conditions can alter mosquito behaviour, terminate reproductive cycles or eliminate the vector. In the former cases, this will limit transmission or, if the unfavourable conditions persist, can prevent the gonotrophic cycle from successful completion, which results in *Anophelism without malaria* (Bruce-Chwatt 1980). 35 ˚C is lethal to most species, however many can remain active amid temperatures as high as 40 ˚C, although the sporogonic cycle will be halted (Muirhead-Thomson 1951; Goma 1966). The lowest survivable temperature is more variable; many *Anopheles* vectors will be killed by prolonged exposure at 5˚C (Ebi *et al.* 2005).

Unfavourable temperatures may, however, be mitigated by behavioural traits. Vectors will rest inside cool shelters to avoid the day-time heat; favouring caves, rock fissures or human shelters depending on the sub-species. Colder temperatures are mitigated through hibernation (also known as diapause) amongst the Palaearctic *Anopheles,* a physiological state of dormancy, which permits vectors to survive the winter months. Some, such as *A. plumbeus*

and *A. claviger*, hibernate as larvae within deep tree holes and pools, both being able to tolerate freezing conditions (Blacklock *et al.* 1920b; Becker 2003). The majority of *Anopheline* vectors hibernate as adults; exophilic vectors seek outdoor shelters, such as caves or earth-barrows, which offer protection against cold or frosty conditions. This behavioural trait can permit the vector to survive extreme temperatures; *Anopheles maculipennis* has been recorded hibernating through temperatures as low as –18 ˚C (Maslow 1930).

Endophilic species favour indoor habitats, seeking warm, dark shelters such as human housing or animal shelters (Balfour 1935; Rice *et al.* 1937; Lividas *et al.* 1941). Studies have shown that indoor temperatures can be several degrees higher than external temperatures; dwellings with multiple occupants will raise the temperature by 1-2 ˚C compared to empty dwellings. This is increased further if fires are lit and kept burning for long periods, or if livestock is kept within or in close proximity to the human dwelling (Haddow 1942; Garnham 1964). Indoor temperatures can allow for the development of malarial *Plasmodiae* when outdoor conditions would not permit their survival, or could only support slower development cycles (Garnham 1964). Vector behaviour can therefore potentially extend the malaria transmission season despite unfavourable climatic trends.

Rainfall is a particularly crucial factor in malaria, not only increasing humidity and consequently the lifespan of the adult mosquito, but also increasing the volume of surface water, which will augment the abundance of viable breeding grounds and increase vector population densities (Bruce-Chwatt 1980). Annual rainfall distribution is, therefore, particularly important in determining the length or virulence of the malarial season; an evenly distributed precipitation regime will result in consistency of breeding grounds and therefore in a more stable mosquito population, while uneven rainfall, as is prevalent in the Mediterranean, will result in unstable malaria patterns (Balfour 1935; Lividas *et al.* 1941; Lindsay *et al*. 1996a). The successful hatching of some *Anopheline* eggs is entirely dependent

on rainfall; *A. plumbeus* lays single eggs on the edge of a tree hole, which will only hatch once the tree hole is flooded. Wet seasons, particularly early in the year, will therefore result in high population densities, increasing the significance of the vector in disease burdens (Becker 2003).

Heavy rainfall can initially be lethal to mosquito populations; *Anopheles* eggs are laid complete with floats to prevent submergence, which causes death (Clements 1963). Flooding or increased rivers currents can, therefore, destroy or sweep existing eggs away and reduce the viability of the water body for oviposition. Mosquito populations will, however, quickly recover from flooding events, as the abundance of mosquitoes is directly related to the volume of surface water (Leishout *et al.* 2004). Once the rains and excess water have abated, the increase in surface water, in the form of small puddles and pools, will quickly be colonised. Mosquito populations tend to be one of the first organisms to extend their range once new areas become environmentally favourable and epidemics are common under such climatic conditions (Bruce-Chwatt 1980; Lindsay *et al.*1996a,b; Patz *et al.* 2000; Leishout *et al.* 2004; Zhou *et al.* 2004; Pascual *et al.* 2006).

The link between rainfall and malaria epidemics has been well noted in recent history (Barber *et al.* 1936a,b; Bouma *et al.* 1996; Singh *et al.* 2002). The typical endemic malaria patterns prevailing in Greece during 1930 transformed into virulent epidemics during 1931 due to unusually high winter rainfall. Spring therefore began with a high volume of surface water and the excess water was not sufficiently evaporated by the heat of the summer months to restrict vector populations to just the drought tolerant species; mosquito populations and infection rates consequently boomed. Barber (*et al.* 1936a,b) noted that epidemic conditions such as these are marked by a considerable increase in *Plasmodium falciparum* infections and a decrease in *P. vivax* and *P. malariae*; mortality rates were consequently particularly high.

The rainfall and volume of surface water levels subsided during the succeeding years and transmission subsequently returned to low to medium endemicity (Barber *et al.* 1936a,b).

It is noted, however, that moisture availability can promote malaria transmission as efficiently as rainfall; studies in China have noted that the frequencies of fog days can provide water, and as a consequence, maintain breeding grounds during periods of low rainfall. Heavy frequencies of fog were shown to result in a delayed effect, causing spikes in transmission up to a year later (Tian *et al.* 2008). Modern climatic studies show that a shallow depression over the western Mediterranean favours the formation of fog across Greece; this commonly occurs at sea level during the summer months, as the water absorbed by the heated air during the daytime is precipitated as fog by night time cooling (Houssos *et al.* 2009). A lack of rainfall, especially along coastal regions, may therefore not necessarily result in a drop in transmission; this would be particularly significant to transmission in Greece during the summer months when precipitation levels are at a nadir (Balfour 1935; Barber *et al.* 1936b; Lividas *et al.* 1941).

Droughts, as with rainfall, can alter transmission rates significantly; while many vectors are intolerant to drought and will be desiccated in low humidity, mild drought can in fact produce favourable conditions for certain vector species, again potentially causing epidemics. Fast running rivers, for example, can be transformed as the currents become slower or even dry completely, leaving just small pools or waterlogged soils in the river bed. Such niches are strongly favoured by some *Anopheles*; *A. superpictus* and *A. sacharovi,* for example, will fill such niches remarkably quickly (Gillett 1971; Leishout *et al.* 2004). Tree hole breeders are often well protected from drought and high evaporation levels, as the tree holes are often deep and the water levels within the hole therefore remain constant; studies have noted that *A. plumbeus* can become particularly abundant during such conditions (Blacklock *et al.* 1920b).

Even species that are largely intolerant to drier conditions will show resilience to mild droughts; the larvae of *A. maculipennis,* for example, can crawl over moist mud for some distance, potentially to find another small pool or puddle of water (Boyd 1949). Severe drought is, however, lethal to mosquito populations; lack of rainfall and low humidity (below 50%) will result in a reduction in the life span of the adult vector and even the desiccation of the vector (Bates 1970). If breeding sites dry up completely *Anopheline* populations will decrease; while some *Culex* mosquitoes will oviposit on moist soils, *Anopheline* mosquitoes are adapted for floating and are easily killed by a lack of water or low humidity (Goma 1966). Prolonged periods of aridity will therefore generally result in a significant decline in the mosquito population.

The climatic conditions of a region will therefore determine the success of the malaria vectors and the efficiency of transmission. The climate of Greece produced one of the longest malarial seasons noted in Europe during the early twentieth century; eight out of twelve months were regularly climatically suitable for oviposition and malaria transmission (Balfour 1935; Lividas *et al.* 1941). Such conductivity, of both climate and environment, gave rise to higher mosquito population densities, higher infection rates and a virulent endemic-epidemic cycle. Studies into malaria patterns in Greece between 1900 and 1960 indicate that a 'typical' malaria pattern began early in the year, as winter or spring rainfall ensured plentiful breeding grounds at the beginning of the malarial season in April. The first vectors to emerge were those that hibernate throughout the winter months as larvae, such as *A. plumbeus* and *A. claviger,* which accounted for an early population peak in spring; early emerging species also include *A. marteri, A. hyrcanus* and *A. superpictus* which increased rapidly in population density throughout spring and into summer. *A. marteri, A. claviger* and *A. hyrcanus* had a second population peak in autumn (Willoughby *et al.* 1918; Balfour 1935; Lividas *et al.* 1941; Belios 1955; Becker 2003; Ponçon *et al.* 2007). *A. sacharovi* and *A. maculipennis*

emerged in mid-spring and in Macedonia were considered “in full career” by mid-April (Rice *et al.* 1937: 169). *A. algeriensis, A. atroparvus, A. hyrcanus* and *A. melanoon* emerged in early summer and increased in population density into late autumn/winter. Vectors with greater drought tolerance would generally prevail throughout the dry summer months; *A. sacharovi* and *A. superpictus* populations reached a peak in August and September and an acute rise in cases was frequently observed in October. The prevalence of vectors would then decline as temperature and light lessens; this generally occurs in autumn, however eggs and larvae from *A. superpictus* and *A. sacharovi* were noted as late as December (Barber *et al.* 1936; Lividas *et al.* 1941).

Transmission was therefore reported to be rare during the winter months; this was particularly the case in the north of Greece where temperatures would regularly drop to 6-7 ˚C although temperatures remained slightly warmer in the south, at c. 9-12 ˚C (Balfour 1935; Lividas *et al.* 1941). Studies noted that mild winters, especially when combined with rainfall, would increase the number of vectors and prolong the transmission season far into the winter months; Balfour (1935) reported infections regularly continuing well into November/December during milder years and primary infection, rather than a relapse, was even noted in February during a particularly mild winter (Balfour 1935; Lividas *et al*. 1941; Ivanova *et al.* 2002; Becker 2003). The parasite burdens of such a transmission season were largely predictable (figure 2.7). *P. vivax* infections would emerge in spring, partly from relapses and partly from new infections; the prevalence would increase during summer and could potentially persist into the winter months if the climatic conditions were suitable. *P. falciparum* would predominate in late summer, autumn and would very rarely persist into winter months, although during mild and wet winters infections were seen as late as February. *P. malariae* did not emerge until summer and autumn but would, again persist into winter given viable climatic conditions (Balfour 1935; Barber *et al.* 1936).

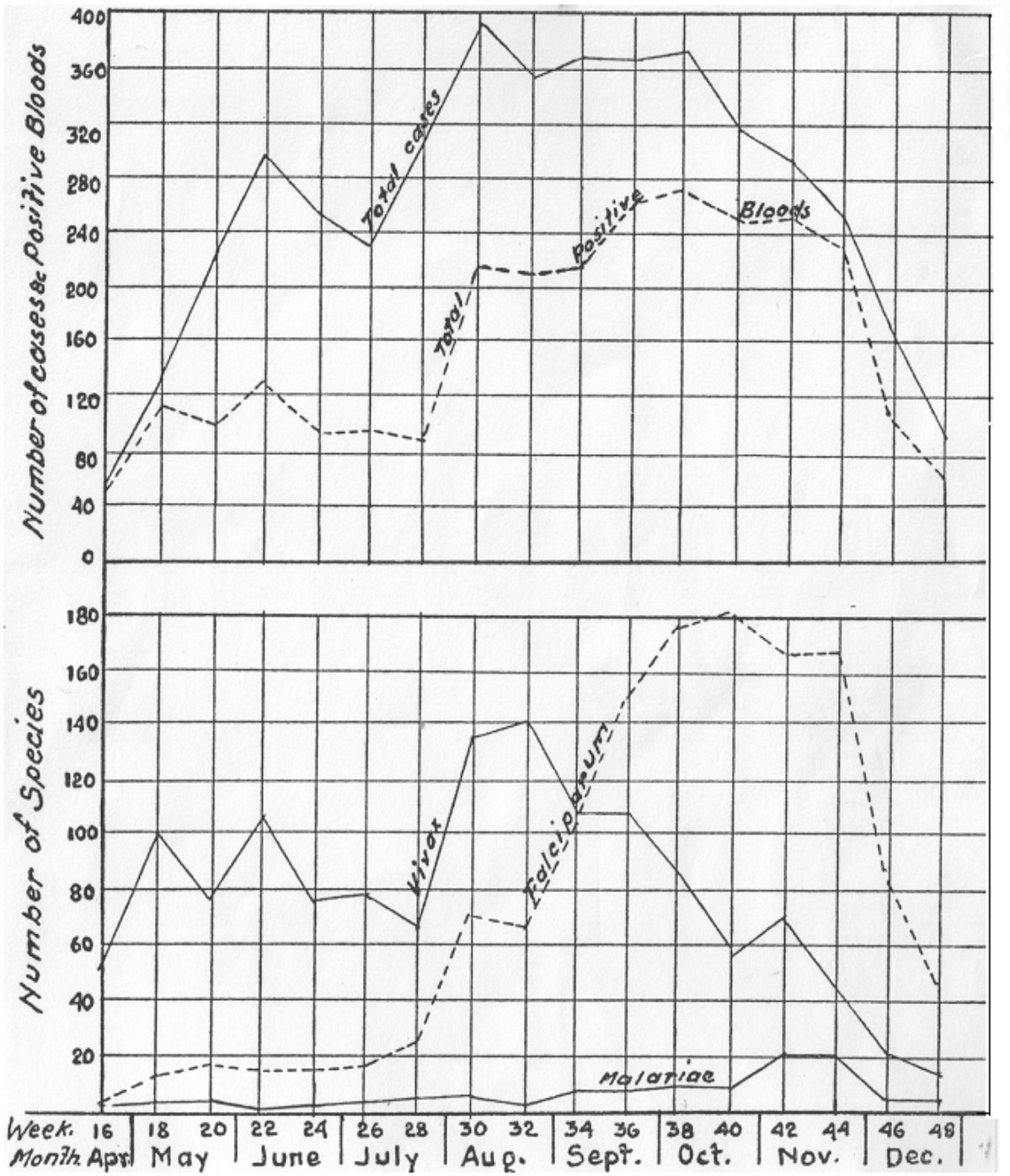


Fig. 2.7: Monthly prevalence of malaria *Plasmodiae* in Greece. Data sourced from three Malaria dispensaries in Greece 1931-1933 (*After* Balfour 1935: chart 2: pg. 326).

These typical disease patterns would alter given varying climatic conditions; even minor variations caused epidemic outbreaks to occur within a larger endemic trend (Balfour 1935; Barber *et al.* 1936a,b). Sequential climatic fluctuations can result in highly destabilized transmission patterns, leading to explosive increases amongst vector populations and therefore potentially to virulent epidemics (MacDonald 1957; Bruce-Chwatt 1980). A recent example of such an interaction occurred in Pakistan in 1993, where an abrupt increase in temperature and rainfall during the late malarial season resulted in a rapid and very notable increase in cases of *P. falciparum* into the winter months (Bouma *et al.* 1994a,b). The endemic transmission of malaria was then punctuated by virulent epidemics. An onset of an epidemic is generally faster with *P. vivax* and *P. malariae* infections; however, an epidemic of *P. falciparum* malaria, although slower in developing, is considerably more damaging (Bruce-Chwatt 1980).

Fluctuating climatic conditions present a particular threat to communities with acquired immunity; as this form of protection needs to be maintained through repeated exposure, an extended hiatus or reduction in transmission will leave a community extremely vulnerable to infection once the climatic conditions ameliorate. Severe epidemics will often follow and mortality rates are generally extremely high (Bruce-Chwatt 1980; Macdonald 1957). The climate is therefore a crucial determinant of malaria; favourable climatic conditions will result in a high vectorial capacity, a term which refers to the number of infective bites received by a host per day or per year. Vectorial capacity is determined by the density of vectors, length of gonotrophic cycle, daily survivorship of the vector, extrinsic incubation period, and the competence of that vector for the malaria parasite(s) (MacDonald 1957). Under optimum temperatures and humidity the efficiency of the endemic vectors peaks, suggesting that transmission would be highly facilitated and infection rates high.

Many of the climatic factors linked to transmission are, however, dictated on a micro-scale. Altitude, rain shadows, prevalence and aspect of breeding grounds and vegetation cover of a given region will influence the effects of the climate and consequently the prevalence of the vector mosquitoes. Reconstructions or predictions of potential malaria patterns therefore require careful consideration of both the general climatic trends and the local environment.

The environment and malaria

Topographical factors such as the positioning and prevalence of hydrological systems, aspect, shelter, soil type and the volume of vegetation cover will determine not only the microclimate but also the malariogenic capacity of the local environment, a term which refers to the viability of the environment for the *Anopheline* vectors. Greece was considered one of the most malarious countries in Europe during the early twentieth century as most of the country suffered from epidemic-endemic cycles of malaria "excepting for very few mountains or insular areas and certain urban centres" (Balfour 1935; 1936; Lividas 1948: 2). Macedonia and Western Greece (Epirus to the Peloponnesus) were however considered the most afflicted regions (Jones 1909; Lividas *et al.* 1941; Belios 1955).

The prevalence of the disease was partly due to the extreme diversity of the Aegean landscape where mountain ranges, valleys, alluvial plains and coastal strips lie side by side (figure 2.8) (Lividas *et al.* 1948). This degree of topographical diversity produces a rich variety of microhabitats which will shelter vectors during times of ecological stress, allowing them to survive and even to thrive, when general climatic trends or environmental conditions become unfavourable. It will also permit different subspecies to co-exist without the need to compete for breeding grounds or shelter; this is a particularly important factor in malaria patterns, as different *Anopheles* subspecies will rarely occupy the same breeding grounds (Horsfall 1955). A variety of *Anopheline* subspecies co-existing within a region can maintain

infection rates during a climatically unviable period; if one vector fails to adapt to climatic or environmental changes, the abandoned niche can very rapidly become colonised by another vector (Patz *et al.* 2000). During the twentieth century the variety of subspecies that coexisted in Greece resulted in extremely high infection rates as the population peaks and respective periods of biting activity of the varied *Anopheles* overlap, which increases the risk of transmission (Lividas *et al.* 1941). Mixed plasmodia infections can also occur due to the multiplicity of vectors, with inhabitants carrying two, or all three plasmodia (Balfour 1935; 1936).

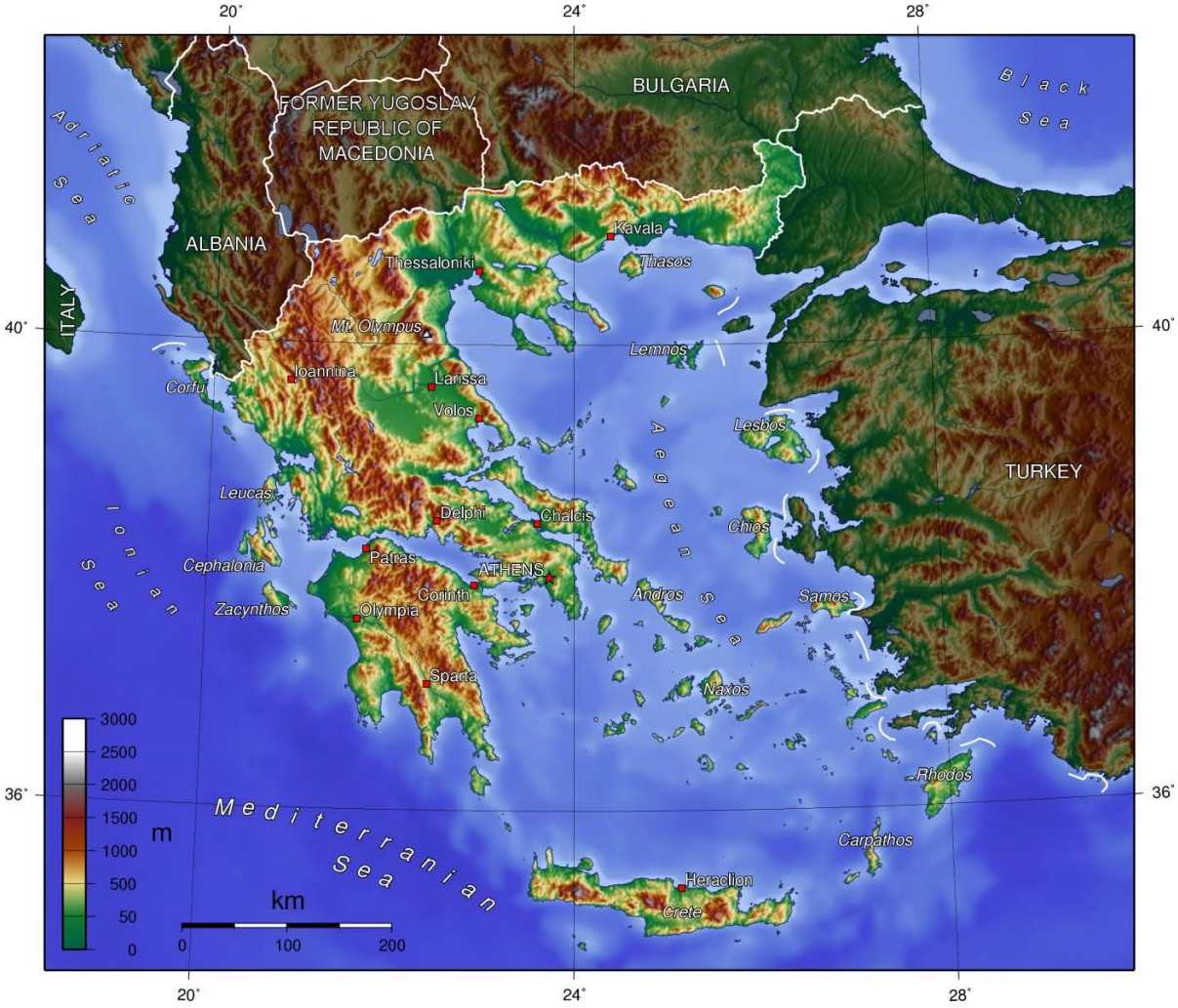


Fig. 2.8: Topographical map of Greece.

Vulnerability to infection is largely delineated by vector ranges; altitude has a broadly indirect relationship with malaria due to the negative correlation between altitude and air temperature (Lindsay *et al.* 1996a). Malaria studies in Greece during the 1930s indicated that communities situated above 250 m altitude had on average a lower infection rate than those that lay below this altitude; an infection pattern that is linked to the prevalence of highly efficient coastal vectors amongst the *Anopheline* vectors of the Mediterranean (Balfour 1935). Hills and mountains have long been recognised as sanctuaries against the prevalence of malaria among the valleys and plains at lower altitudes; seasonal migrations to higher elevations are therefore common in malarious regions with a diverse topography (Balfour 1936; Lindsay *et al.* 1996a,b).

Some vectors have a highly varied habitat range, which extends from sea level to altitudes of 2000 m; the primary vector *A. sacharovi* can, for example, successfully transmit malaria at 1000 m in altitude (Balfour 1935; Lividas *et al.* 1941; Bruce-Chwatt 1980). The range of a sub-species' habitat is however partially dictated by intra-species competition; studies have shown that habitats will broaden if vectors do not have to compete for breeding grounds. *A. sacharovi*, for example, will move inland in the absence of competition despite a predominantly coastal dispersal (Becker 2003). The range of a vector can also be altered through climatic fluctuations; temperatures will vary considerably from year to year which can increase the geographical range of the vectors, causing infection to occur at higher altitudes. Vectors can expand their habitats to higher elevations; *A. superpictus* is historically renowned for this, often breeding in water collections on plateaus or in mountain streams (Lividas *et al.* 1941; Becker 2003). Malaria studies have noted that this can potentially result in severe epidemics, as the communities at higher elevations will lack immunity (Garnham 1948; Lindsay *et al.* 1996a,b).

Hydrological systems are the most significant environmental factor in malaria disease patterns; the positioning of a water body in relation to a settlement is crucial with regards to infection rates, as the female vector will readily bite when seeking a suitable breeding ground (Le Menach *et al.* 2005). Vector flight ranges are generally limited to 5-6 km from a viable breeding ground, although *A. atroparvus* have been shown to fly up to 10 km, representing the furthest recorded *Anopheles* flight (Bates 1970). A village or town lying within this distance of a favourable water collection will, therefore, increase the probability of infection (Leishout *et al.* 2004; Le Menach *et al.* 2005). Marshland, swamps and bogs have long been equated with virulent malaria, as many of the *Anopheline* vectors breed prolifically within stagnant waters of high organic content; this association has been recorded as early as the fifth century BC (Hippocrates *Airs, Waters and Places*). *A. sacharovi* and *A. superpictus,* primary vectors in Greece during the twentieth century, as well secondary vectors such as *A. maculipennis, A. hyrcanus* and *A. atroparvus,* all favour lentic (still or stagnant) breeding grounds. Mosquito population density and as a consequence infection rates in the locality of such water bodies is frequently high (Sabatinelli 2002).

Studies have shown, however, that marshland is not a pre-requisite of malaria, as the varied vectors of Greece in fact favour highly diverse forms of water bodies (figures 2.9) (Balfour 1935; Lividas *et al.* 1941). Lotic environments, such as the margins of rivers, streams and springs, are strongly favoured by many of the *Anopheline* vectors; some prefer shaded areas where surrounding vegetation breaks up the currents, such as *A. algeriensis, A. hyrcanus, A. maculipennis* and *A. plumbeus* (Blacklock *et al.* 1920b; Becker 2003). Others, such as *A. superpictus* and *A. sacharovi,* tend to prefer sunlit waters and are therefore often better suited to water bodies within cleared and cultivated land; human exposure to these vectors is greater than that of the shade-loving vectors and, as a consequence, the contribution of sun-loving mosquitoes to transmission is more significant (Becker 2003).

Many *Anopheline* vectors will also colonise brackish waters. *A. superpictus, A. atroparvus, A. algeriensis* and *A. sacharovi,* are all tolerant of saline waters, although *A. sacharovi* is the most tolerant, being able to oviposit in waters of very high salinity (Yaghoobi-Ershadi *et al.* 2001). Settlements in coastal regions in proximity to high volumes of brackish water, most particularly salt marshes, but also water bodies such as rock pools, are therefore at particularly risk of infection due to the prevalence of these extremely virulent mosquitoes (Lividas *et al.* 1941; Yaghoobi-Ershadi *et al.* 2001). Some vectors thrive within transient water collections, such as shallow pools of water, water-filled animal footprints or submerged depressions within the soil (Bruce-Chwatt 1980). Vectors that favour such ephemeral pools are particularly dangerous as their preferred breeding grounds are readily available in most environments, from woodland, agricultural or pastoral regions to urban contexts. These vectors can persist even during the hotter, drier seasons when the breeding grounds of other vectors disappear. *A. superpictus,* for example, is historically extremely prevalent during dry periods in the eastern Mediterranean, breeding in residual pools of water and dried up streams; the vector is particularly prevalent in dried up gravel streams along valley floors (Balfour 1936; Lividas *et al.* 1941; Sabatinelli 2002). *A. claviger* and *A. algeriensis* are equally opportunistic with temporary water collections, strongly favouring water filled animal footprints; while not considered to be as virulent as *A. superpictus*, the population density of these sub-species can increase rapidly and the vectors can contribute significantly to malaria burdens (Kasap 1987; Şimşek 2006). *Anopheline* vectors that favour ephemeral water bodies can often breed prolifically within urban contexts, breeding in any shallow pools of water along drains, gutters and even in man-made containers (Bruce Chwatt 1980).

Vector	Marshes/ Swamps	Rivers/ Streams	Ponds/ Pools	Brackish Water	Fresh Water	Temporary Collections	Tree Holes
A. algeriensis	X			X	X	X	
*A. atroparvus**	X	X	X	X	X		
*A. claviger**		X	X		X	X	
*A. hyrcanus**	X	X	X	X	X	X	
A. maculipennis s.s		X	X		X		
A. marteri		X			X		
A. melanoon	X	X	X		X		
*A. plumbeus**					X		X
A. sacharovi	X	X		X	X	X	
A. subalpinus	X	X			X		
A. superpictus	X	X		X	X	X	

Fig. 2.9: Most common breeding grounds of *Anopheline* vectors. **Bold** indicates primary vectors; Asterisk indicates secondary vectors.

Vectors	Urban water collections	Irrigation systems	Sunlit	Shaded	Vegetation	Altitude	References
A. algeriensis				X	X	Coastal vector	Lividas *et al.* 1941; Becker 2003
*A. atroparvus**	X	X	X		X	Coastal vector	Lividas *et al.* 1941; Becker 2003
*A. claviger**	X	X	X		X	Sea level to 2000 m	Lividas *et al.* 1941; Becker 2003
*A. hyrcanus**		X	X		X	Coastal vector	Becker 2003; Ponçon *et al.* 2007
A. maculipennis s.s		X		X		Sea level to 2300 m	Balfour 1935; Lividas *et al.* 1941; Becker 2003.
A. marteri		X		X		Coastal to 1000 m	Aitkin 1953; Becker 2003
A. melanoon			X			Coastal to 400 m	Becker 2003
*A. plumbeus**	X			X	X	Sea level to 2000 m	Blacklock *et al.* 1920b; Becker 2003
A. sacharovi	X	X	X			Sea levels to 1000 m	Lividas *et al.* 1941; Becker 2003
A. subalpinus			X		X	Sea level to 1200 m	Postiglione *et al.* 1973; Becker 2003
A. superpictus	X	X	X			Sea level to 1200 m	Lividas *et al.* 1941; Becker 2003

Fig. 2.9 cont'd.

The rarity of some *Anopheline* habitats can limit their significance with regards to malarial transmission; for example vectors that favour tree holes in deforested regions, or those that favour isolated habitats, have minimal exposure to humans or to urban settings. Studies show, however, that where these habitats become prevalent and conditions are favourable, the vector's contribution to infection rates increases considerably due to increased vector population densities (Blacklock *et al.* 1920b; Becker 2003). The contribution of these 'rarer' vectors to malaria patterns is further augmented by an ability to adapt to urban environments; *A. plumbeus*, has been found breeding in isolated trees within urban settings (Blacklock *et al.* 1920b; Shute *et al.* 1974), and, along with *A. claviger* and *A. atroparvus*, has been noted to colonise urban water bodies with high organic contents, including sewage systems, drainage and wells (Blacklock *et al.* 1920b; Aitkin 1954).

Anopheles and the urban environment

Urbanization, even on a small scale, will directly affect the prevalence and distribution of vector species, as man-made environments can protect vectors against unfavourable climatic and environmental conditions. Only certain species are however adapted to anthropogenic environments (figure 2.10), the behavioural traits of which increase the degree of contact between vector and the human host and consequently increase the contribution of the vectors to malaria patterns. *A. sacharovi* and *A. superpictus* were the primary vectors of the Greek *Anopheline* vectors due to high population densities and to marked anthropogenic tendencies; the marked endophilic (preferring to shelter within human and animal shelters), endophagic (preferring to bite indoors) and anthropophilic (preferring human blood) behaviour caused the vectors to remain within human environments both night and day, thereby augmenting infection rates. *Anopheles* vectors primarily bite during the crepuscular period but will continue to bite, to one degree or another, throughout the night; this increases the risk of infection as endophilic species will attack sleeping human hosts (Bates 1949; Becker 2003).

Vectors will also bite during the day if their rest is disturbed and human activities within the household or animal shelters can increase the risk of transmission further (Becker 2003).

Secondary vectors display less human oriented habits, choosing to bite or rest outdoors, or favouring animal blood over that of humans. *A. maculipennis,* for example, has historically been considered as a lesser vector than *A. superpictus* or *A. sacharovi* as, although endophilic and endophagic, *A. maculipennis* displays zoophilic tendencies and will shelter within animal stables rather than human dwellings (Barber *et al.* 1935; Becker 2003). *A. atroparvus* and *A. melanoon* display similar behavioural traits, suggesting that these vectors also play a lesser role in transmitting malaria. Studies have however demonstrated that most *Anopheline* vectors are in fact highly opportunistic feeders; in the absence of the preferred host, the vectors will readily feed on a convenient host (Sabatinelli 2002; Saul *et al.* 2003). Zoophilic vectors may therefore bite humans and are able to contribute to the malarial burden, particularly if population densities are high, as is often noted in both *A. melanoon* and *A. maculipennis* (Balfour 1935; Barber *et al.* 1935; Sabatinelli 2002; Saul *et al.* 2003).

Exophilic (favouring outdoor resting places) and exophagic vectors (displaying outdoor biting habits) generally constitute secondary or highly irregular vectors, as contact with humans is limited. *A. hyrcanus,* a common sub-species in Greece, was considered to have played a minor role in malaria patterns due to predominantly outdoor resting and biting habits (Lividas *et al.* 1941; Kaiser *et al.* 2001). Extreme population densities of *A. hyrcanus,* or increased contact due to changes in human behaviour, could however increase the significance of the vector as it is strongly anthropophilic and has been found to be both endophagic and endophilic during the spring; the vector can therefore occasionally contribute to the malaria burden (Lividas *et al.* 1941; Ponçon *et al.* 2007).

Vector	Endophilic (Human)	Endophilic (Animal)	Endophagic	Exophilic	Exophagic	Anthropophilic	Zoophilic	Vector Significance	Reference
A. algeriensis				++	++	+	+	**Rare**	Becker 2003
A. atroparvus	(+)	++	++			+		**Potential**	Lividas *et al.* 1941; Becker 2003
A. claviger s.s	(+)		(+)	++	++	+	++	**Potential**	Lividas *et al.* 1941; Şimşek 2006
A. hyrcanus	(+)		(+)	++	++	++		**Secondary**	Ponçon *et al.* 2007; Becker 2003
A. maculipennis s.s	+	++	+			+	++	**Primary/ Secondary**	Balfour 1935; Lividas *et al.* 1941; Becker 2003
A. marteri		+	+	++	++	+	++	**Rare**	Hadjinicolaou 1938
A. melanoon	+	++	++			+	++	**Rare**	Lividas *et al.* 1941
A. plumbeus *			(+)	++	++	++		**Secondary**	Blacklock *et al.* 1920b; Becker 2003
A. sacharovi	++	++	++			++		**Primary**	Balfour 1935; Lividas *et al.* 1941
A. subalpinus		++	+	+	+		++		Becker 2003
A. superpictus	++	++	++	+		+	+	**Primary**	Balfour 1935; Lividas *et al.* 1941; Becker 2003

Fig. 2.10: Behavioural traits of the *Anopheline* vectors of Greece. Key: (+)- rare; +- occasional; ++ - strong behavioural trait.

Similarly, a potential for exceptionally high population densities of *A. claviger* increases importance of this vector, despite predominantly exophagic and exophilic tendencies (Blacklock *et al.* 1920b; Postiglione *et al.* 1973). *A. plumbeus*, despite a woodland habitat, will also enter human dwellings to feed (Blacklock *et al.* 1920b). All three of these exophilic vectors can therefore be considered as viable malaria vectors.

Other Greek *Anopheline* species do not contribute as significantly to the malarial burden due to strict exophilic, exophagic behaviour, strong zoophilic tendencies and predominantly small population numbers. This combination of habits lessens the frequency of contact with humans; *A. subalpinus* and *A. marteri* are such vectors and, although receptive to malaria parasites, their contribution to malaria burdens is therefore minimal (Lividas *et al.* 1941; Becker 2003). These vectors are not therefore considered further within this thesis.

The urban environment therefore increases the risk of infection, as endophilic vectors are strongly attracted to man-made constructions; such as housing, animal shelters, and man-made water systems. The planning, materials and construction of these edifices will determine the vulnerability of the human inhabitants to infection. In the case of housing, studies have shown that tiled roofs and brick walls prevent mosquitoes from accessing the interior of the buildings, while more basic materials such as mud or clay bricks and thatched roofs are highly favourable to vectors (figure 2.11) (Barber *et al.* 1935; Ye *et al.* 2006). Mud-lined walls or roofs develop cracks and these, as well as gaps amongst reeds or rushes, are favoured shelters for *Anopheles* vectors, providing protection from predators and shelter from the elements. Most significantly, however, such materials permit the vectors to enter the building in search of a blood meal (Barber *et al.* 1935; Lindsay *et al.* 2002; Ye *et al.* 2006). The design of the house will also determine the accessibility for mosquitoes; the presence and

size of eaves, positioning of the windows and doors are all significant factors (Lindsay *et al.* 2002).

Fig. 2.11: Image of an Eastern Macedonian house from the 1930s. Constructed with thatched roof and whitewashed mud-brick walls. High numbers of endophilic and endophagic vectors were recorded in these houses in comparison to tiled and brick dwellings (*After* Barber *et al*. 1935: fig. 2: pg. 514).

These constructions can furthermore provide microclimates and microenvironments that can protect vectors from unviable conditions in the natural environment, as internal temperatures can exceed the external temperatures significantly, permitting rapid development and even extended transmission seasons (Garnham 1964). Due to the relatively limited flight dispersal of the vectors, the location of a house will affect the accessibility and therefore the prevalence of *Anopheline* vectors within indoor environments (Bates 1970). Houses positioned in close proximity to water bodies, animal shelters, other houses, agricultural areas or on the edge of large urban settlements are most vulnerable to vector invasion.

Urban water systems offer many of the *Anopheline* vectors, even some rural species, viable breeding grounds; wells, cisterns, sanitation and drainage channels have all been linked to increases in urban vector density. Even water filled man-made containers such as pottery vessels are favoured breeding grounds for some vectors (Bruce-Chwatt 1980). These anthropogenic water collections supply constant volumes of surface water which can potentially support extended larval habitats and will furthermore provide protection for the *Anopheline* larvae and eggs against many of the natural predators, leading to high population densities (Patz *et al.* 2000; Keiser *et al.* 2005). Natural accumulations of water, such as ponds, lakes, rivers and marshland expose the aquatic stages of *Anopheline* to insects, bats, fish and aquatic birds, which help to limit the mosquito density. Mosquitoes are highly vulnerable to predators in the early stages of their lifecycle and, although adult vectors are preyed upon, the predators of *Anopheline* larvae and eggs are particularly pivotal in restricting vector populations (Becker 2003). Man-made water collections will lack many of these predatory species and vector populations are consequently able to increase. These water collections can therefore pose a severe threat to a community.

The presence of domesticated animals within urban settings has been shown to have significant effects on infection rates, as vectors with zoophilic tendencies can be deflected away from the human populations onto the animals in which the parasites cannot amplify. The ratio between the animals and the human population is therefore crucial; should the size of the herds outnumber the inhabitants, the transmission rate amongst the human population would theoretically be reduced. Some studies have shown that the deliberate stabling of animals in proximity to areas in which humans sleep, a practice known as zooprophylaxis, is an efficient method of reducing infection rates; pastoral societies and livestock-based societies may therefore be at a lower risk of disease (McNeil 1975; WHO 1982). However, the efficacy of this theory has recently been questioned (Bouma *et al.* 1995; Bøgh *et al.* 2002;

Saul 2003). Studies have shown that the stabling of cattle in proximity to the sleeping quarters of the household could actually augment infection rates. The zoophilic vectors of the area were attracted to cattle but instead of being diverted away from the human inhabitants would feed upon sleeping humans en route to the stabled animals. Convenience, rather than host preference, it appears, is of priority to a hungry vector.

Studies have furthermore shown that the vector lifespan can increase considerably when livestock are easily accessible; the highest mortality rate in the adult mosquito lifecycle occurs when seeking food. The provision of livestock will therefore facilitate vector feeding, increasing the chances of survival (Killeen *et al.* 2004). This will have an enormous impact on transmission rates, as a longer lifespan will result in further feeding, and further generations of mosquitoes. It is therefore concluded that domesticated animals can serve to increase the risk of malarial infection (Saul *et al.* 2003; Killeen *et al.* 2004).

Urban malaria is therefore largely associated with poor planning; a well-structured and regulated community will not suffer from severe infection rates, if overcrowding is avoided and water sources and sanitation systems are well designed and maintained. A poorly designed, disorganised settlement with 'primitive' facilities and materials can however result in high infection rates. The quality of living conditions, including factors such as overcrowding, poor housing standards, unregulated waste disposal, badly maintained water and drainage structures or poor sanitation systems will encourage vector breeding and biting behaviour within the settlement confines, increasing the contact between vector and human host. A particular danger is posed by collections of water polluted with a high organic content, such as sewage, drainage systems or water collections containing household rubbish, will increase the favourability of the water body as breeding grounds, providing hiding grounds to protect the larvae (Mitchell *et al.* 2008). These living conditions can furthermore

increase the susceptibility of inhabitants to infection by weakening immune systems (Bruce-Chwatt 1980).

Despite the facilitation of the urban environment for some malaria vectors, it is generally noted that smaller, rural communities are more susceptible to malaria infection than larger, more complex urban sites. Firstly, the rural setting will potentially expose the community to all the *Anopheline* vectors, rather than just the urban adapted mosquitoes, which increases the probability of infection. Secondly, the abundance of clean and shallow water bodies in rural, coastal and agricultural regions will support a greater density of *Anopheline* mosquitoes and thirdly, the social or economic activities of these areas will expose the communities to a greater number of areas with a high malariogenic capacity. Historically, these smaller communities are considered to be at a greater risk of infection (Lividas *et al.* 1941; Becker 2003; Robert *et al.* 2003).

Malaria and ecological change

Ecological changes can initiate dramatic fluctuations in mosquito population densities and habitat range (Yasuoka *et al.* 2007; Pattanayak *et al.* 2008). Anthropogenic activities, such as deforestation, agriculture, road construction, development of water systems, mining and expanding urbanisation have a profound effect on ecosystems and are strongly linked to alterations in mosquito distribution and malaria patterns (figure 2.12) (Patz *et al.* 2000). Deforestation, in particular, has strong repercussions on malarial vectors, affecting aquatic systems, microclimate, shade, soil stability, pH levels and the ecology of the local fauna and flora. Such changes will have a strong impact on the incubation period of the various malarial parasites and the daily survival, breeding patterns and biting rates of the vectors (Patz *et al.*

2000; Pattanayak *et al.* 2008). The loss of forest cover alters the albedo[20] of soil and water bodies due to increasing air movements, altered humidity regimes and reduced shade, causing daily average temperatures of open land to vary from those of dense forests by up to 10 ˚C (Ricklefs *et al.* 1999). This increase in temperature can increase the vectorial capacity for mosquitoes that favour sunlit waters and open landscapes, such as *A. sacharovi* and *A. superpictus,* by decreasing the development time of the vector, leading to greater population densities and, most significantly, by shortening the incubation period of the malaria parasites.

The removal of vegetation root systems will also reduce the absorption capacity of the soil and increase the vulnerability to erosion. The resulting increase in surface water availability is closely linked to sharp increases in vectors that favour sunlit breeding grounds which, in Greece, includes the most virulent and efficient of all the *Anopheline* vectors, *A. sacharovi* and *A. superpictus* (Leishout *et al.* 2004). Water bodies will also become increasingly viable for oviposition due a change in pH levels; forest floors that are covered with leaf litter have highly acidic soils, causing water collections to be unfavourable to most vectors. The removal of trees causes the pH levels of the soils to fall to a more neutral level, thereby increasing the viability of the water body for the majority of *Anopheline* vectors (MacGregor 1929). The loss of organic litter from ponds within forested regions particularly favours the primary vectors, *A. sacharovi* and *A. superpictus,* which cannot tolerate eutrophic conditions (Patz *et al.* 2000; Kampen *et al.* 2003). The reduction in ecological diversity associated with environmental changes will therefore cause the population density of the primary vectors to increase, while *Anopheline* vectors that oviposit in shaded water bodies or favour woodland habitats, such as *A. maculipennis* and *A. plumbeus,* will decrease in prevalence.

[20] The albedo of an object is a measurement of a surface's diffuse reflectivity

The effects of deforestation upon infection rates depend upon the pre-existing disease patterns; in non-endemic regions or amongst populations with high immunity, the repercussions of land clearance are unlikely to be severe. In endemic regions, deforestation has however been linked to epidemic outbreaks as the increased environmental and climatic viability of the cleared region results in a higher vectorial capacity (Patz *et al.* 2000; Pattanayak *et al.* 2008). Land clearance can, furthermore, result in a geographical expansion of the disease, as populations within the previously unviable areas will tend to lack immunity due to minimal, or no, prior exposure to the disease; these populations are therefore highly vulnerable to infection (Norris 2004; Pattanayak *et al.* 2008).

Environmental Change	**Potential Vector Increase**	**Potential Vector Decrease**	**References**
Deforestation, land clearance and construction	*A. claviger*, *A. melanoon*, *A. sacharovi*, *A. superpictus*	*A. plumbeus* *A. hyrcanus*, *A. atroparvus* *A. algeriensis*, *A. maculipennis*	Lividas *et al.* 1941; Becker 2003
Land cultivation and exploitation	*A. claviger*, *A. hyrcanus*, *A. sacharovi*, *A. atroparvus* *A. superpictus*, *A. maculipennis*,	*A. plumbeus*, *A. algeriensis*	Lividas *et al.* 1941; Becker 2003

Fig. 2.12: Ecosystem changes and effects on *Anopheles* population density

Agriculture is considered a great catalyst for enhancing *Anopheline* populations; however, even in the absence of ecological changes associated with land clearance, the most fertile regions are often the most malarious. Floodplains or alluvial soils along rivers and lakes for example create highly productive soils that support crop cultivation with minimal labour, while the abundance of water in the form of waterlogged soils, pools or shallow water along the river margins, can support dense vector populations (Lividas *et al.* 1941; Sherratt 1980;

Becker 2003). Such fertile regions were particularly exploited in early prehistory as the regions required little to no deforestation or soil preparation for cultivation (Sherratt 1980; Wilkie *et al.* 1997).

Agricultural development may enhance the malariogenic capacity of such landscapes further. Cultivation and disruption of soils can alter natural waterways, increasing the sedimentation of streams or rivers; this will transform fast running currents into slower water flows and simultaneously decrease the depth of the water, creating conditions which favour most *Anopheline* vectors (Norris 2004). The construction of irrigation channels, canals and ditches will provide further viable breeding grounds and can also increase groundwater levels, resulting in water logging in adjoining areas (Keiser *et al.* 2005; Le Menach *et al.* 2005). These expanses of surface water are furthermore likely to be sunlit due to land clearance, strongly favouring *A. sacharovi, A. superpictus* and *A. maculipennis* which are strongly linked to cultivated areas of land, although *A. atroparvus, A. claviger* and *A. hyrcanus* are also common within such environments (Becker 2003).

Construction projects associated with expanding settlements or economic bases, such as the development of road systems or mining industries, can similarly create viable habitats for the primary vectors. The clearance or extraction of soils can result in severe erosion, causing water to pool on the surface and interfere with existing hydrological systems, thereby altering breeding grounds (Patz *et al.* 2000). The construction of roads is particularly significant in disease patterns; firstly due to land disturbance, and secondly due to the facilitation for increased population movements between urban settlements. This can lead to severe epidemics as unexposed populations will lack immunity and, most significantly, the clone-specific and mutation-specific nature of premunition renders populations vulnerable to *Plasmodiae* strains from an adjacent region (Babiker *et al.* 1997; Freitas-Junior *et al.* 2000).

The construction of roads and associated population movements may therefore initiate severe outbreaks of disease even within populations with well-established immunities.

Reconstruction of malarial burdens on past civilisations

It is surmised, based on these modern malarial studies, that the early societies of Greece would have been highly vulnerable to malaria if the disease was extant within Greece during these periods. The hunter-gatherer societies of the Mesolithic would perhaps be at the least risk of infection due to a lack of anthropogenic influence on the landscape; however, exposure to the existing vector habitats would theoretically be high due to the wide use of the resource bases in food sourcing. The social and economic evolution of the early societies between the Neolithic and Late Bronze Age, encompassing the agricultural revolution and the development of the first urban centres, would be expected to have had significant effects on ecological systems, altering the malariogenic capacity of these regions considerably and increasing the risk of infection. The small subsistence communities of the Neolithic, which would lack long-term food storage facilities, health infrastructures, sophisticated sanitation systems or construction materials, would indicate a high vulnerability to infection, while the development of the first urban centres, expansive trade routes and large scale agriculture during the Bronze Age would be suggested to have augmented vector densities, expanded the geographical distribution of the disease and heightened the risk of infection. Theoretically, it is suggested that if a settlement was within a region of high malariogenic capacity, vulnerability to the disease would have been high. Malaria could have exacted a heavy toll on these early societies that would influence day- to- day life in both social and economic terms.

There is, however, a large level of uncertainty surrounding any attempt to reconstruct disease patterns of the past; the complexity of the relationship between the climate, environment, anthropogenic environments and malaria, coupled with the scarcity of archaeological

evidence pertaining to these early periods, precludes definite conclusions as to malarial patterns from being drawn. As shown above, malaria patterns are dictated by climate, environment and by both *Anopheline* and human behaviour, factors which are largely implemented on a micro-scale; successful transmission may depend upon the volume of shade or the organic content of a water body, daily temperature fluctuations, or upon the frequency of suitable resting places in proximity to a settlement. These factors remain, however, invisible within the archaeological record. Palaeoclimatology, for example, cannot reconstruct weather patterns; daily, monthly or even annual fluctuations are rarely visible and only decadal to centennial trends of temperature, humidity and precipitation can be reconstructed. Malaria *patterns* cannot be determined from this data but this approach can help to ascertain whether the general climatic trends could have supported malaria. Micro-environmental factors are equally obscured to archaeological reconstructions and the fine details of transmission patterns during prehistory will therefore elude us; however many of the significant environmental factors in the malariogenic *capacity*, such as hydrological systems and topography can be reconstructed with comparative confidence. These techniques, along with archaeological reconstructions of settlements, economic and social behaviour will be applied in order to ascertain whether the malaria parasites and the more virulent of the *Anopheline* vectors could have survived in early prehistoric Greece.

In order that this may be achieved, the tolerances and behavioural patterns of the historical vectors of Greece will be used as a direct reference, as it is assumed by scholars that these vectors would have been present over the past ten millennia and that their behavioural patterns have remained constant (Bruce-Chwatt *et al.* 1980; de Zulueta 1994). Modern malaria studies will be referred to in attempting to ascertain whether malaria would have presented a threat to the populations of Franchthi cave, Nea Nikomedeia and Lerna. It is noted that comparisons with modern malarial studies are similarly fraught with difficulties

due to the seemingly infinite variables that influence transmission patterns, many of which remain invisible within an archaeological record. References to these studies are therefore made with caution.

Having outlined the epidemiology and main determinants of malaria, reconstructions of the malariogenic capacity of the Greek mainland between the Mesolithic and Late Bronze Age will now be attempted. The palaeoclimatic conditions of the Aegean during the periods in question will be reconstructed first, in order to ascertain the general climatic trends and their favourability for malarial transmission. The environmental conditions of the three archaeological sites will then be considered in chapters four to six.

Chapter Three:

Malaria and the Aegean climate: Mesolithic to the Late Bronze Age

Angel (1964; 1971; 1972; 1973) hypothesised that the climatic conditions of the Aegean between the Mesolithic and Late Bronze Age were highly conducive for endemic malarial transmission, suggesting that the malarial *Plasmodiae* were introduced into the Aegean during the Mesolithic period, while the genetic immunity β-thalassemia was introduced with migrating populations from the Near East during the Late Palaeolithic period. Angel (1972) further suggested that the climatic patterns of the Mesolithic to Late Bronze Age were strong contributing factors in the fluctuating frequencies of the genetic immunity amongst these prehistoric populations. In light of recent advances in palaeoclimatology, this chapter will attempt to trace, in so far as is possible, the general climatic trends over the Mediterranean in order to consider firstly, whether the climatic conditions of the Aegean during the Mesolithic were conducive for the introduction of the malarial *Plasmodiae* and the associated vectors. Secondly, this chapter will attempt to determine what effect the climatic patterns of subsequent archaeological periods would have had upon potential malarial transmission. The aim is therefore to determine whether a palaeoclimatic reconstruction would support Angel's (1966; 1971; 1973) hypothesised frequencies of malaria transmission during the prehistory of the Aegean (see chapter one).

Methods

Reconstructions of the palaeoclimate of the early Holocene involve the analysis of proxy data; these are local and regional records that are interpreted using physical or biophysical principles to represent climate-related variations in the past. Climatic proxy data include: tree-rings, speleothems, pollen records, vertebrate fossils, ice cores, lake and marine

sediments, geological and geomorphological features (Cronin 1999) (figure 3.1). Proxy data sources have varying strengths and weaknesses with regards to climatic reconstruction and dating which must be considered before an interpretation of the data is attempted.

Sources of Proxy Data for Palaeoclimatic Reconstruction		
Geochemical	***Biological***	***Physical***
Carbon Isotopes	Seeds	Shoreline
Stable Oxygen Isotope	Pollen	Bathymetry
	Diatoms	Sedimentology
	Vertebrate	Geomorphology

Fig. 3.1: Sources of proxy data referred to within the thesis.

Pollen cores are one of the most important proxy data sources for inferring past climatic and environmental conditions, potentially permitting the reconstruction of regional or local (site-specific) conditions. There are, however, many caveats to the interpretation of this reconstructive technique. The taphonomic processes that lead to the deposition of the samples are highly significant to interpretation, and the catchment area of the coring sites must be established. Marine and lakes cores will receive pollen from considerable distances through aeolian or fluvial transport, leading to the representation of regional rather than local taxa, while cores from bogs tend to reflect more local plant communities (Larsen *et al.* 1993). Pollen distribution will also vary between different plant species; *Pistacia* (L.) (pistachio) and *Tilia* (L.) (lime), for example, both major climatic indicators, produce very little pollen in comparison to other arboreal species such as *Pinus* (L.) (pine) or *Quercus* (L.) (oak). These imbalances, unless addressed, can lead to under, or over, representation within the pollen

record (Rossignol-Strick 1995). Vegetation responses to climatic or ecological changes are furthermore slow and fluctuations in taxa species may reflect an environmental or climatic change that occurred long before the deposition of the pollen. Anthropogenic activity can also obscure climatic or environmental changes, as land clearance or farming can result in significant changes to the pollen frequencies; as a consequence, pollen cores cannot be used as a secure indication of climatic conditions during later prehistoric periods when human activity increased in prevalence. Careful interpretation of pollen records is therefore crucial (Cronin 1999).

Producing a reliable and robust chronology from terrestrial pollen cores is also subject to difficulties. The resolution of pollen records varies considerably; lake sediments are often composed of annual layers which can provide an annual resolution, however, the rate of sedimentation must be considered when dating of the core is attempted. The application of radiocarbon dating can be limited by poor preservation conditions and, in the eastern Mediterranean, can be hampered by the hard water effect in limestone regions which increases the radiocarbon age by c. 1200 years (Rossignol-Strick 1995; Bell *et al.* 2005). All radiocarbon dates within this thesis have been corrected to account for the hard water error.

The mineral component of marine sediments can provide climatic data at a potentially high resolution. Terrestrial sediments are transported by air and are washed into the ocean from riverine environments; the formation and composition of these sediments can be used to indicate climatic conditions. Sapropel depositions, for example, are layers of organic-rich sediment in the Mediterranean, that reflect increased monsoonal activity over Africa, leading to augmented precipitation levels and amplified riverine-runoff (Rossignol-Strick *et al.* 1982; Rohling 1991). The biogenic components of marine sediments, formed of plants, animals and single-celled organisms, can also be used to infer fine intra-annual records of oceanic

variability (Cronin 1999).

The most informative proxy data from marine cores are *foraminifera;* these single-celled organisms are highly sensitive to temperature and, by comparing the distribution and diversity of fossil foraminifera species with modern assemblages, these species can be used to infer sea surface temperatures (SSTs) of past periods. SSTs, although lagging behind air-over-land temperature by several months, may in turn be used to infer general temperatures. *Planktonic* foraminifera, organisms living near the surface of the water, are considered to be more representative of air-over-land temperatures than *benthic* foraminifera, which live within the bottom sediments and are more reflective of sea-surface temperatures. SSTs can also be inferred through UK-37 analysis, a technique which measures concentrations of alkenone; the abundance of this biomarker, produced in the cell structure of marine algae, is directly correlated with SSTs (Cronin 1999; Bradley 1999). As these algae live near the water surface, they are closely correlated to air-over-land temperature (Cronin 1999). Studies of oxygen isotope values (the ratio of ^{16}O to ^{18}O, referred to as $\delta^{18}O$) in fossil foraminifera can also be used to infer temperature and humidity levels in past periods. Lighter oxygen (^{16}O) evaporates from the ocean during cooler conditions resulting in higher ^{18}O values, while warmer phases of low evaporation cause increased levels of ^{16}O (Bradley 1999; Cronin 1999). $\delta^{18}O$ values of marine environments can, however, alter in interglacial and glacial periods and interpretations of $\delta^{18}O$ values are therefore made with caution (Cronin 1999; Rohling *et al.* 1999).

The radiocarbon dating of marine sediments is subject to similar difficulties as terrestrial pollen cores. There is a significant reservoir effect due to a delay in exchange rates between atmospheric CO_2, ocean bicarbonate and a dilution effect caused by the mixing of surface waters with up-welled deep waters, causing the radiocarbon age of terrestrial and marine

cores to vary by approximately 150-700 years. A correction must therefore be applied in order to account for this difference (Stuvier *et al.* 1993). A reservoir age correction has been applied to all marine cores referred to within this thesis. The resolution of marine sediments can be low due to the slow accumulation of sediments and biogenic mixing; however chronological correlations between terrestrial and marine data sets can be achieved through identifiable stratigraphic formations, such as volcanic sediments (Bradley 1999; Cronin 1999).

Stable isotope analysis can also be applied to speleothems, calcareous deposits such as stalagmites, stalactites and flowstones, formed from dripping water within caves. Measurements of oxygen and carbon isotopes ratios[1] ($\delta^{8}O$ and $\delta^{13}C$)[21] from these calcite formations and the thickness of the depositional layers are extremely successful techniques in reconstructing precipitation and temperature fluctuations on a local scale (Bradley 1999). Climatic reconstructions based upon speleothem records may be compromised by the potentially variable nature of cave environments; this can be accounted for by measuring the consistency of $\delta^{8}O$ and $\delta^{13}C$ values in both the fossil sample and within the modern calcite deposits from the cave (Bradley 1999). Speleothems are dated through $^{230}Th/\ ^{234}U$ thermal ionization mass spectrometry (TIMS); a method which is considered more accurate than radiocarbon dating in periods exceeding 9000 years before present; these are absolute ages and no correction is needed (Bard *et al.* 1990; Bradley 1999).

Sedimentological studies are used to reconstruct both ancient landscapes, including hydrological systems, vegetation cover and anthropogenic influences, and to indicate climatic variability. Soil characteristics vary with prevailing climatic and environmental conditions,

[21] $\delta^{13}C$ ratios: interpreted as changes in overlying vegetation (C_3 versus C_4 plants: groups which contain different ratios of carbon atoms) and vegetation density. Interpretations as to precipitation and temperature are therefore based on modern knowledge of the tolerances of these vegetation groups (Cronin 1999; Bradley 1999).

including aeolian and fluvial influences, moisture availability and temperature. The identification of sedimentary and diagenetic processes, including erosion, bioturbation and cryoturbation, can therefore be used to indicate climatic and environmental dynamics. Cave sediments are of particular use to palaeoclimatic and environmental reconstruction due to a potentially high temporal resolution, a local or site-specific scale of reconstruction and a high possibility of favourable preservation. Stratigraphic disturbance can also occur through anthropogenic activity, erosion or environmental change, which can complicate interpretations. Radiocarbon dating terrestrial sediment cores is subject to similar limitations as that of pollen cores in the eastern Mediterranean, being dependant on the availability of suitable organic material and potentially affected by the hard water error (Cronin 1999).

Dendroclimatology is a particularly efficient method for reconstructing palaeoclimatic conditions; samples can not only provide robust chronological sequences, as trees grow in annual increments, but can also provide high resolution data on a local, or micro-scale. Tree rings can be used to infer temperature, precipitation, sunlight and wind, as the width of a ring will vary depending on the favourability of the prevailing conditions; narrow rings indicating stressful or unsuitable conditions and wide rings reflecting viable conditions. The limitations to this technique lie in the variable factors that can affect ring growth: non-climatic factors include soil types, age of the tree, fire, density of the vegetation community, genetic differences, anthropogenic disturbance, herbivore impact (particularly sheep grazing), pest outbreaks, disease and CO_2 concentration. Careful interpretation of the evidence and, where possible, correlations with other data sets are therefore required (Bradley 1999; Cronin 1999).

Faunal remains, especially of small mammals and invertebrates, can provide excellent sources of proxy data. Many species, especially of invertebrates, have very narrow climatic and environmental tolerances and their identification can be used to reconstruct past

conditions at a small temporal resolution. Birds and large mammals with seasonal migrations can indicate seasonal temperature ranges, while species with low mobility, such as some species of rodent, reptile and invertebrate, are extremely useful in reconstructing environment and climatic conditions on a micro-scale (Cronin 1999). Carbon isotopes from faunal remains represent a further method for determining environmental conditions; ratios of $^{12}C/^{13}C$ ($\delta^{13}C$) within snail shells can provide information on the type of plants consumed by the snails, which can be used to infer environmental changes (Goodfriend 1999). Dating these proxy sources relies upon archaeological correlations with datable stratigraphic layers; radiocarbon dating is subject to suitable preservation.

The problems surrounding high-resolution dating and the relative insensitivity of the majority of the available proxy data to micro-scale events results in insufficiently detailed climatic information for specific malaria seasons or transmission patterns to be identified. Although single, dramatic events may be identified through some proxy data sources, such as sedimentological studies or dendroclimatology**,** weather patterns which are expressed on a day-to day basis cannot be reconstructed, and even annual or decadal fluctuations may be difficult to identify. The limitations of this approach are recognised, as general climatic trends cannot be used to draw definitive conclusions as to disease patterns. As Hackett (1937) and Sallares *et al.* (2004) have noted, malarial transmission patterns are enacted on a micro-scale and can, therefore, only be positively determined by micro-analysis; mosquito vectors are relatively limited in their geographical range and their success is therefore entirely dependent on local climate patterns, environment, hydrological systems and host populations. General climatic trends are still important to malarial transmission; a microclimate may protect against a mild decrease in humidity, however a several hundred year drought or a 2-4 ˚C drop in temperature will have significant ramifications on disease patterns, regardless of microclimatic conditions. The reconstruction of general climatic trends, supplemented by the

available proxy data which are sensitive to local-scale changes, will therefore permit Angel's (1966; 1971) theory of a high malariogenic capacity during the Mesolithic to Late Bronze Age to be tested; although a hypothesis as to exact disease patterns cannot be achieved, such reconstructions can determine whether conditions could have supported the disease and the disease vectors. Reconstructions of transmission patterns made within this thesis will only be attempted where the resolution of the proxy data is sufficiently high; any conclusions as to disease patterns remain highly theoretical.

In reconstructing the climatic trends of the Aegean, data will be drawn from mainland Greece, the Aegean and the wider region of the eastern Mediterranean. The climatic conditions of the Younger Dryas, the climatic event which ended prior to the beginning of the Mesolithic period[22], will also be considered as these climatic conditions are important in helping to ascertain whether the malarial *Plasmodiae* and the genetic immunity, β-thalassemia, could have become established as early as the Mesolithic period. The climatic data for each chronological period, from the Mesolithic to the end of the Bronze Age, will then be examined with reference to the archaeological sites in question: Franchthi Cave, Southern Argolid (Mesolithic-Middle Neolithic), Nea Nikomedeia, Northern Greece (Early to Middle Neolithic) and Lerna, Argive Plain (Early to Late Bronze Age) (figures 3.2a-c). The potential effects on malarial patterns will then be evaluated and compared to Angel's (1972; 1973; 1986) human skeletal evidence and suggested frequencies of β-thalassemia. It must further be noted that other important factors in malaria transmission, such as environment, population dynamics and migrations are not discussed in any detail within this chapter.

[22] This transition is dated with reference to the radiocarbon dating of Franchthi Cave: see figure 3.2a

Chronology

All dates within this chapter are presented in calibrated years BP and BC. In all cases, 'BP' stands for 'years before 1950 AD', based on the 5730-year half-life of ^{14}C. 'Raw ^{14}C yr. BP dates will be listed in footnotes; where unavailable in the original studies, these have been taken from Reimer (*et al.* 2004). 'Cal. BP' represents the calibrated age of the BP date derived from dendrochronology; all calibrations are made to 2σ (95% probability) unless otherwise stated and all reservoir corrections have been made. Cal. BC is the 'cal. BP' age minus 1950 years.

Chronological Phase	Lab Sample	^{14}C age	Cal. BP 2σ	Cal. BC 2σ	Median cal. BC	Chronological period cal. BC (Perlès 2001)	Reference
Lower Mesolithic	P-2227 P-2103 P-2102 P-2108 P-2228 P-1518 P-1517	9430±160 9300±100 9290±100 9250±120 9060±110 8940±100 9030±110	11166-10290 10735-10243 10721-10241 10740-10199 10554-9833 10250-9698 10494-9779	9217-8341 8786-8294 8772-8282 8791-8250 8605-7884 8301-7749 8545-7830	8762 8543 8530 8493 8272 8079 8225	8700- 8000	(1,3,4)
Upper Mesolithic	P-1666 P-2096 P-2107	8740±110 8710±100 8530±90	10155-9538 10150-9529 9732-9303	8206-7589 8201-7580 7783-7354	7832 7781 7569	8000-7000	(1,3,4)
Final Mesolithic	P-1536 P-1526	8190±80 8020±80	9408-8996 9123-8631	7459-7047 7174-6682	7214 7053		
Initial (Aceramic) Neolithic	P-2095 P-2094 P-1527 P-1392	7980±110 7930±100 7900±90 7790±140	9189-8544 9029-8521 9007-8541 9002-8372	7240-6595 7080-6572 7058-6592 7053-6423	6889 6838 6803 6674	7000-6450	(1,3,4)
Early Neolithic	P-1525 P-1667 P-1399	7700±80 7280±90 7190±110	8636-8371 8315-7950 8302-7788	6687-6422 6366-6001 6353-5839	6540 6152 6069	6450-5900	(1,3,4)
Middle Neolithic	P-2093 Beta-15613 P-2235 P-1662 P-1824 P-1537 Beta-15614 Beta-15612	6940±90 6860±120 6750±80 6690±90 6670±70 6650±80 6720±100 6600±250	7942-7617 7941-7509 7749-7464 7671-7435 7656-7434 7658-7427 7757-7428 7958-6960	5993-5668 5992-5560 5800-5515 5720-5480 5707-5485 5709-5478 5808-5479 6009-5011	5829 5765 5660 5610 5591 5580 5637 5536	5900-5300	(1,2,3,4,5)

Fig. 3.2a. Chronology of Franchthi Cave from Mesolithic-Middle Neolithic occupation. Calibrated by author using OxCal 4.1. **(1)** Jacobsen *et al.* 1987 **(2)** Gifford 1990 **(3)** Perlés 2001; (**4)** Reingruber *et al.* 2005. (5) Vitelli *et al.*

Chronological period cal. BC in northern Greece (Andreou *et al. 1996*)	Lab Sample	^{14}C age	Cal. BP σ 2	Cal. BC	Median cal. BC	Ref.
Early Neolithic **6700/6500-5800/5600**	**Q-655**	**8180±150**	**9481-8658**	**7532-6709**	**7188**	**(1)**
	GX-679	**7780±270**	**9397-8048**	**7448-6099**	**6715**	**(1)**
	P-1202	**7557±91**	**8540-8186**	**6591-6237**	**6414**	**(1)**
	OxA-1606	**7400±100**	**8387-8018**	**6438-6069**	**6274**	**(1,2)**
	OxA-1605	**7400±90**	**8379-8028**	**6430-6079**	**6277**	**(2)**
	OxA-4282	**7400±90**	**8379-8028**	**6430-6079**	**6277**	**(1,2)**
	OxA-3874	**7370±80**	**8353-8018**	**6404-6069**	**6242**	**(1,2)**
	P-1203A	**7281±74**	**8302-7956**	**6353-6007**	**6149**	**(1,2)**
	OxA-3873	**7300±80**	**8313-7968**	**6364-6019**	**6163**	**(1,2)**
	OxA-3876	**7370±90**	**8366-8014**	**6417-6065**	**6242**	**(2)**
	OxA-1604	**7340±90**	**8348-7981**	**6399-6032**	**6206**	**(1,2)**
	OxA-3875	**7280±90**	**8315-7950**	**6366-6001**	**6152**	**(1,2)**
	OxA-4283	**7260±90**	**8311-7934**	**6362-5985**	**6137**	**(1,2)**
	OxA-4281	**7100±90**	**8157-7721**	**6208-5772**	**5972**	**(1,2)**
	OxA-1603	**7050±80**	**8007-7703**	**6058-5754**	**5926**	**(1,2)**
	OxA-4280	**6920±120**	**7970-7572**	**6021-5623**	**5924**	**(1,2)**

Fig. 3.2b. Early Neolithic occupation of Nea Nikomedeia, Plain of Veria, Northern Greece. **1)** Pyke *et al.* 1996, **2**) Perlés 2001, **3)** Reingruber *et al.* 2005. Calibrated with OxCal 4.1. Dates Q-655 and GX-679 are considered aberrant due to an uncertain provenance and, in the case of GX-679, a large standard deviation. These samples are therefore commonly rejected (Bintliff 1976; Perlès 2001; Weninger *et al.* 2006).

Relative phase of the Bronze Age	Site Phase	Relative chronological Phase	Chronological period cal. BC (Manning 1995)	Lab Sample	^{14}C age	Cal. BP Cal. BC σ 2		Median cal. BC	Ref
Early Bronze Age	Lerna III	Early Helladic II (EHII)	2650/2450 -2200/2150	P-318 P-319 P-321 P-320 P-300 P-312 GrA-28046	4070±72 3980±66 3940±68 3930±65 3870±61 3840±72 3830±35	4821-4420 4798-4236 4569-4155 4528-4155 4437-4092 4430-3993 4408-4099	2872-2471 2849-2287 2620-2206 2579-2206 2488-2143 2481-2044 2459-2150	2638 2500 2428 2413 2346 2304 2283	(1,2,3)
	Lerna IV	Early Helladic III (EHIII)	2200/2150-2050/2000	P-303A P-299 GrA-28051 GrA-28213	3750±112 3750±97 3730±35 3640±45	4432-3831 4414-3877 4225-3977 4086-3846	2483-1882 2465-1928 2276-2028 2137-1897	2175 2173 2130 2009	
Middle Bronze Age	Lerna V	Middle Helladic I (MH)	2050/2000-1950/1900	GrA-28054 GrA-28045	3595±35 3585±35	4062-3779 3983-3731	2113-1830 2034-1782	1952 1940	
Late Bronze Age		(MHII)	1950/1900-1750/1720	GrA-28050 GrA-28039 GrA-28048 GrA-28041 P-303 GrA-28211 GrA-28157 GrA-28160	3560±35 3545±35 3535±35 3530±35 3520±59 3510±50 3475±40 3440±40	3970-3722 3959-3716 3907-3700 3898-3700 3970-3641 3913-3621 3842-3640 3831-3590	2021-1773 2010-1767 1955-1751 1949-1751 2021-1692 1964-1692 1893-1691 1882-1641	1909 1887 1865 1848 1844 1832 1804 1753	
		(MHIII)	1750/1720-1680	No radiocarbon samples taken for Lerna VI or VII					
		Late Helladic I (LHI)	1680-1600/1580						
	Lerna VI	LHIIA	1600/1580-1520/1480						
		LHIIB	1520/1480-1445/1435						
	Lerna VII	LHIIIA	1435-1360						
		LHIIIB	1360-1200						

Fig. 3.2c. Bronze Age occupation of Lerna, Argive Plain. *After* **1)** Kohler *et al.* 1961, **2)** Ralph *et al.* 1962, **3)** Voutsaki *et al.* 09. Calibrated with OxCal 4.1.

The Younger Dryas (c. 10750- 9050 cal. BC/12700-11000 cal. BP) [23]

The transition to the Mesolithic was preceded by a cold and arid climatic trend known as the Younger Dryas, one of the last cooling phases of the Late Glacial Maximum which is noted to have occurred across Europe, the Near East, Africa, Asia and the Mediterranean (Cronin 1999; Bar-Matthews 1999; Alley 2000; Rohling *et al.* 2002; Geraga *et al.* 2005; Rosen 2007). Proxy data from across the Aegean and the eastern Mediterranean (figure 3.3) show that temperatures and precipitation levels were significantly reduced during this period resulting in near glacial conditions, with pronounced cooling and highly arid conditions (Rohling *et al.* 2002; Geraga *et al.* 2005; Kuhnt *et al.* 2007). Planktonic foraminifera and UK-37 analysis from core LC21 and core MNB-3 respectively indicate that SSTs were 4-5 ˚C lower than the modern; winter SSTs in the southern Aegean remained below 12.5 (figure 3.4), considerably lower than the modern mean winter SST of >16˚C, while the mean annual SST of the northern Aegean Sea remained at c. 17˚C , again considerably lower than the modern value of 22 ˚C (Poulos *et al.* 1997; Rohling *et al.* 2002; Gougou *et al.* 2007).

Increases in $\delta^{18}O$ in marine cores C69 and LC21 indicate a contemporary phase of pronounced aridity; this is supported by pollen records from Ioannina, Lake Xinias, Tenaghi Philippon and marine pollen cores SL148 and SL152 in the north of the Greek mainland, which indicate a predominance of taxa such as *Artemisia* and Chenopodiaceae. These desert taxa, noted in pollen cores across the eastern Mediterranean, survive in regions of less than 100 mm of annual precipitation, indicating pronounced aridity (Bottema 1974; 1995; Rossignol-Strick 1995). Dead Sea levels, $\delta^{18}O$ and $\delta^{13}C$ values from speleothems in the Levant indicate that these cooling and arid conditions extended over much of the eastern Mediterranean (Yechieli *et al.* 1993; Bar Matthews *et al.* 1999).

[23] 10620±33 ^{14}C yr BP - 9560±21 ^{14}C yr BP (Alley *et al.* 2000; Wilson *et al.* 2008)

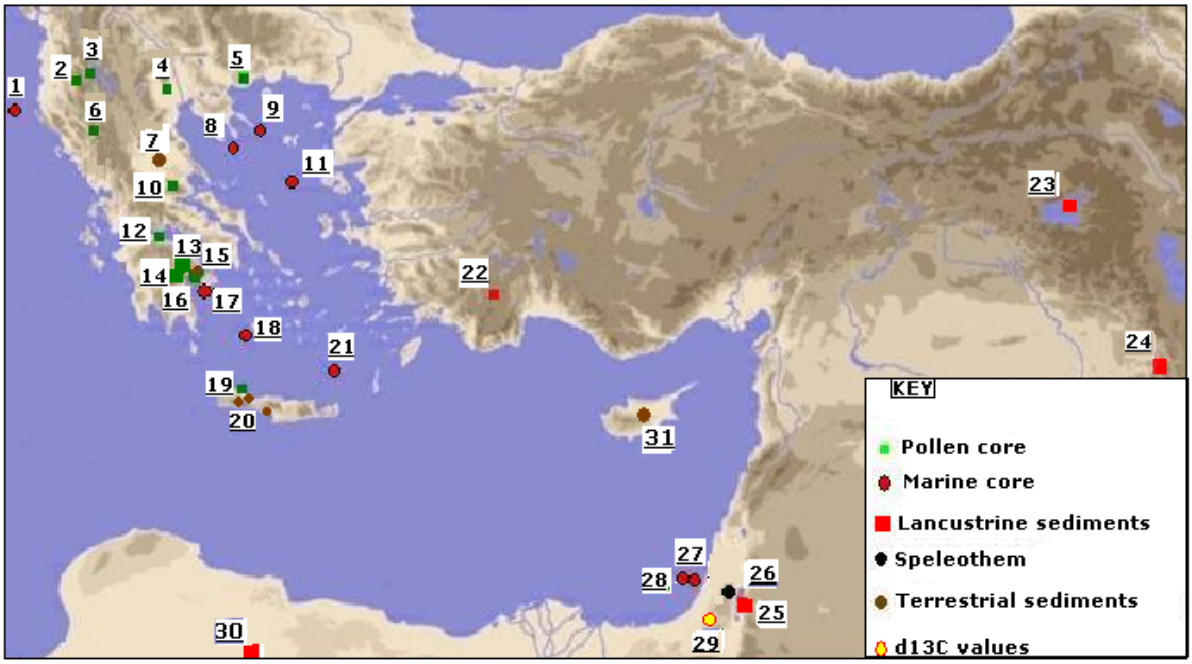


Fig. 3.3. Map showing sources of proxy data mentioned in the text.

1. Core AD91-17 (Sangiorgi *et al.* 2003), **2.** Rezina Marsh (Willis 1992b), **3**. Gramousti Lake (Willis 1992a), **4.** Lake Giannitsa (Bottema 1974), **5.** Tenaghi Philippon (Wijmstra 1969; *et al.* 1976), **6.** Ioannina Basin (Lawson *et al.* 2004), **7.** Theopetra Cave (Karkanas 2001), **8.** Core GeoTü SL152 (Kotthoff *et al.* 2008a,b), **9.** Core GeoTü SL148 (Kotthoff *et al.* 2008a,b), **10.** Lake Xinias (Digerfeldt *et al.* 2000), **11.** Core MNB-3 (Gougou *et al.* 2007), **12.** Aliki Lagoon (Kontopoulos *et al.* 2003), **13.** Kleonai (Atherden *et al.* 1993), **14.** Lake Lerna (Jahns 1993), **15.** Sediment Core Argive Plain (Zangger 1993), **16.** Kiladha Bay (Bottema 1990), **17.** C-40 (Geraga *et al.* 2000), **18.** C69 (Geraga *et al.* 2005), **19.** Tersana (Bottema *et al.* 2003), **20.** Frangokastello, Khania and Agios Vailieous (Moody 2005), **21.** Core LC-21 (Rohling *et al.* 2002), **22.** Gölhisar Gölü (Eastwood *et al.* 1999), **23.** Lake Van (Wick *et al.* 2003), **24.** Lake Zeribar (Stevens *et al.* 2001), **25.** Dead Sea levels (Enzel *et al.* 2003), **26.** Soreq Cave (Bar-Matthews *et al.* 1997; 1999), **27/28.** GA110 and GA112 (Schilman *et al.* 2001), **29.** Negev Desert (Goodfriend 1999), **30.** Western Fezzan (Gasse 2000), **31.** Dhali-Potamia, Cyprus (Butzer *et al.* 2007).

Global climatic studies indicate that the Younger Dryas underwent several warming interruptions, where temperatures abruptly increased by c. 1.5 ˚C and humidity levels increased (Kobashi *et al.* 2008); it has been further suggested that the aridity and cooling of the period may have been a seasonal phenomenon in some regions (Dormoy *et al.* 2009). The comparison of fossil pollen from core SL152 in the northern Aegean Sea to modern pollen distributions indicate that the temperature decrease was not as marked during the summer months, while precipitation levels were higher in both the spring and summer months (Denton *et al.* 2005; Kotthoff *et al.* 2008a; Dormoy *et al.* 2009). The seasonality of the

Younger Dryas may, therefore, have permitted warmer, more humid periods across the Aegean.

The duration of the event appears to have varied from area to area. A general global termination date of c. 9550-9050 cal. BC (11500-11000 cal. BP)[24] is suggested (Alley *et al.* 1993; 2000). Palaeoclimatic evidence may suggest that the cooler conditions may have persisted in central Greece. Micromorphological studies of sediments from Theopetra cave indicate strong freeze-thaw activity, suggesting a period of cooler, arid conditions which two secure radiocarbon dates place at 11220-10710 cal. BC (13170-12660 cal. BP) and 10690-8210 cal. BC (12630-10150 cal. BP)[25] (Karkanas 2001; Facorellis *et al.* 2001), while foraminifera analysis from marine core LC21 in the Cretan basin (figure 3.4) indicates that the near glacial conditions continued until c. 9050-8550 cal. BC (c. 11000-10500 cal. BP)[26] within the Aegean (Rohling *et al.* 2002). These latter dates from LC21 are considered to mark the beginning of the Holocene period and broadly coincide with the emergence of the Mesolithic period at Franchthi Cave in the Southern Argolid (figure 3.2a) (Perlès 2001).

The Mesolithic Period (8700-7000 cal. BC/ 10650-8950 cal. BP)

The termination of the Younger Dryas was marked by an abrupt climatic amelioration, where conditions across the eastern Mediterranean rapidly increased in warmth and humidity. $\delta^{13}C$ and UK-37 analysis from marine core MNB-3 in the northern Aegean Sea indicate that mean annual SSTs increased by 5 ˚C, from 17 ˚C to the modern mean SST value of 22 ˚C (Poulos *et al.* 1997; Gougou *et al.* 2007). The application of Modern Analogue Technique (MAT) on pollen cores from SL148 and SL152 in the northern region, indicate that mean winter temperatures also increased to those of the modern, averaging at c.

[24] 10033±16-9560±21 ^{14}C yr BP (Alley *et al.* 1993)
[25] 10971±87 and 9721±390 ^{14}C yr BP respectively (Facorellis *et al.* 2001)
[26] 9560±21 ^{14}C yr BP -9283±17 ^{14}C yr BP (Reimer *et al.* 2004)

6 ˚C (Gougou *et al.* 2007; Kotthoff *et al.* 2008b); planktonic foraminifera analysis from LC21 core off the north of Crete indicates that by c. 8550 cal. BC (10500 cal. BP)[27] temperatures from the southern Aegean had reached a minimum of 16 ˚C, equal to those of the modern SSTs of the Levantine region (figure 3.4) (Poulos *et al.* 1997; Rohling *et al.* 2002).

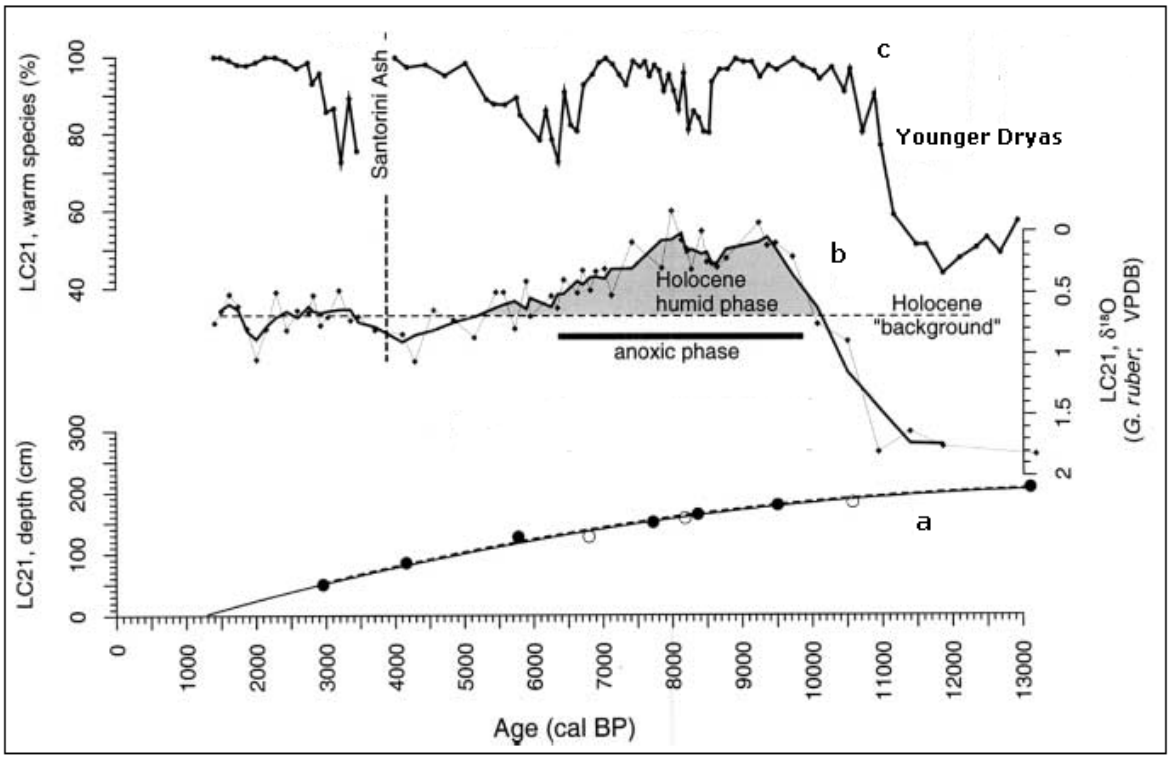


Fig. 3.4. Data from marine core LC-21.

(A) Black dots indicates seven AMS ^{14}C dates from the core, open dots are dates from nearby core SL31, correlated into LC21 on the basis of high resolution foraminiferal records. An Aegean reservoir age correction of 150 years is applied. **(B)** Oxygen isotope record for the summer mixed-layer dweller *Globigerinoides ruber*. The Holocene background is approximated at about the mean value of the last 2 kyr covered by the record. The grey marks the enhanced freshwater flux into the Mediterranean during the monsoonal maximum. The black bar indicates the extent of anoxic sedimentation (Sapropel deposition) **(C)** Warm-cold plot for LC21, showing Holocene cool events representing relative winter SST reductions of the order of 2-4˚C. 100% reflects the modern day temperatures of the Levantine basin (a minimum of 16 ºC); 80% represents conditions similar to the modern day SST of the north Aegean Sea (12-14 ºC) (*After* Rohling *et al.* 2002: fig. 1: 588).

[27] 9283±17 ^{14}C yr BP (Reimer *et al.* 2004)

Oxygen isotope studies from speleothems within the Levant and $\delta^{13}C$ and $\delta^{18}O$ studies on snail shells from the Negev desert indicate that the transition to the Holocene was marked by increased precipitation levels, which persisted until the Early Neolithic period, in c. 6250 cal. BC (8200 cal. BP)[28] (Goodfriend 1991; Bar-Matthews *et al.* 1999). Lacustrine sediments from Lake Van in Anatolia and Western Fezzan, North Africa and $\delta^{18}O$ values from calcite deposits at Gölhisar Gölü in Anatolia support this contention, indicating considerably higher humidity and rainfall levels during the early Holocene than those of the modern (Gasse 2000; Wick *et al.* 2003; Eastwood *et al.* 2007). Higher precipitation levels are also suggested for the Greek mainland; winter precipitation levels in c. 8550 cal. BC (c. 10500 cal. BP)[29], determined by modern analogue functions of pollen records from SL152 in the Thermaic Gulf, were at c. 215 mm and were rapidly rising. This represents the lowest recorded levels for the early Holocene within this core; however between 1958 and 1994 AD, the mean winter rainfall of Thessaloniki was 117 mm. In comparison with the modern precipitation values, 215 mm therefore constitutes an "extremely wet" season (Kutiel *et al.* 1996: 76; Xoplaiki *et al.* 2000; Kotthoff *et al.* 2008a).

Pollen signals from marine core SL152, Lake Xinias and Ioannina also reflect an increase in moisture; the transition from the arid and cold conditions of the Younger Dryas is clearly marked by a steady increase in broad-leaf taxa including *Quercus* (L.), *Tilia* (L.), *Corylus* (L.), (hazel), *Ulmus* (L.), (elm) and *Acer* (L.) (maple) (Bottema 1974; Rossignol-Strick 1995; 1999; Digerfeldt *et al.* 2000; Kotthoff *et al.* 2008a). Pollen records from marine core C-40 and C-69 in the southern Aegean indicate a contemporary change in vegetation as the coniferous vegetation of the drier, colder conditions of the Glacial Maximum reduced in favour of *Olea* (L.) (olive) and *Pistacia* (Geraga *et al.* 2000). This change in taxa would

[28] 7415±18 ^{14}C yr BP (Reimer *et al.* 2004)
[29] 9283±17 ^{14}C yr BP (Reimer *et al.* 2004)

suggest a transition to frost free winters and increased annual rainfall distribution (Rossignol-Strick 1995; Geraga *et al.* 2000; 2005). Seismic profiling of a river bed, partially submerged in Kiladha bay, lying to the west of the Franchthi headland in the Southern Argolid, also reflects elevated precipitation rates; analysis indicates that the river discharge during the Mesolithic period (c. 8700-7000 BC, see figure 3.2a) was three to four times that of the modern. These increased levels persisted until c. 5050-4050 BC (7000/6000 BP) (these are inferred dates based on sedimentation rates and the general eustatic sea level curves for the Aegean; no radiocarbon dates are available for this event) (van Andel *et al.* 1980; Perlès 2001). Precipitation levels continued to increase during the Mesolithic Period; modern analogue functions of pollen records from cores SL148 and SL152 from the Thermaic Gulf indicate that winter precipitation regimes and humidity levels of the northern Aegean remained stable at c. 210 mm until c. 7550 cal. BC (c. 9500 cal. BP)[30] when they increased to an average of 300 mm, levels which are considered highly elevated compared to present day conditions (Kutiel *et al.* 1996; Xoplaiki *et al.* 2000; Kotthoff *et al.* 2008a).

Proxy data from the Mediterranean would therefore indicate a distinct decline in seasonal variance and a transition to a far milder climate at the beginning of the Holocene period; the warmer and wetter conditions appear to have remained stable for an exceptionally prolonged period, continuing for approximately two millennia (Geraga *et al.* 2000; Rohling *et al.* 2002; Kotthoff *et al.* 2008a, b; Kuhnt *et al.* 2008). SSTs largely remained stable at >16 ˚C and 6 ˚C in the southern and northern regions respectively between c. 9050-8550 cal. BC (c. 11000-10500 cal. BP)[31] and c. 6250 cal. BC (8200 cal. BP)[32], with no major fluctuations evident in the proxy records (Rohling *et al.* 2002; Geraga *et al.* 2000; 2005; Kotthoff *et al.* 2008a).

[30] 8492±17 ^{14}C yr BP (Reimer *et al.* 2004)
[31] 9560±21 ^{14}C yr BP- 9283± 17 ^{14}C yr BP (Reimer *et al*. 2004)
[32] Commonly dated to 7400±100/ 7805±40 ^{14}C yr BP (reservoir correction of 400 years) (Weninger *et al.* 2006; Kotthoff *et al.* 2008a).

The favourability of these elevated humidity and precipitation levels for both the *Anopheles* vector and for the *Plasmodiae* would therefore appear high and is suggested to have been augmented still further by the beginning of the 'Early-Holocene Humid Phase' (hereafter referred to as 'HHP'), dated to c. 7050 cal. BC (c. 9000 cal. BP)[33] (Rossignol-Strick 1995; 1999; Rohling *et al.* 2002) (figure 3.4). This well-recorded climatic trend of increased precipitation levels occurred across north Africa, the Near East and the Mediterranean and lasted until the beginning of the Early Bronze Age at c. 3000 cal. BC (4950 cal. BP)[34]. This wetter phase is clearly delineated by the deposition of sapropel 1, noted in both the southern and northern marine cores from the Aegean Sea. This organic-rich layer of sediment, commonly dated to c. 7050/7550 cal. BC (c. 9500/9000 cal. BP)[35], was caused by amplified riverine run-off and increased precipitation levels over the Mediterranean; the deposition of this sediment has been linked to enhanced African Monsoon activity and indicates higher precipitation levels than those of the modern (Rohling *et al.* 1991; De Rijk *et al.* 1999; Rossignol-Strick 1999; deMenocal *et al.* 2000).

Pollen cores from across the Mediterranean indicate that vegetation altered significantly in conjunction with this warmer and wetter trend, entering what Rossignol-Strick (1999) has termed the *Pistacia* phase. Marine pollen records from C-40, C-69, SL152 (dated with reference to the deposition of sapropel 1), and well-dated terrestrial pollen records from Ioannina, Lake Xinias and Tenaghi Philippon indicate that *Pistacia* and deciduous pollen, such as *Ostrya* (Scop.) (hornbeam), *Fraxinus* (L.) (ash), *Ulmus* and *Tilia,* became abundant as the HHP began (Rossignol-Strick 1995; 1999; Digerfeldt *et al.* 2000; Geraga *et al.* 2005; Kotthoff *et al.* 2008a). These species are moisture loving, indicating frost-free winters, warm

[33] 8056±13 ^{14}C yr BP (Reimer *et al.* 2004)
[34] 4580±40 ^{14}C yr BP (reservoir correction of 500 years) (deMenocal *et al.* 2000)
[35] 8492±17 ^{14}C yr BP / 8056±13 ^{14}C yr BP (Reimer *et al.* 2004)

summers and increasing precipitation (Kotthoff *et al.* 2008a). The wetter phase is furthermore evident in pollen records from the Ghab valley in Syria, Lake Van in Turkey and Lake Hula in Northern Israel, which indicate that drier taxa, such as *Ephedra* (L.) (joint-pine), *Artemisia* (L.) (wormwood) and coniferous forests, gave way to deciduous forests and increasing volumes of broad-leaf species (Rossignol-Strick 1999; Wick *et al.* 2003; Rosen 2007). The Mesolithic occupation of Franchthi Cave ended within this climatic phase, in c. 7050 cal. BC (9000 cal. BP) (figure 3.2a) (Jacobsen 1973; 1981; Perlès 2001).

The climate and the malariogenic capacity of Franchthi Cave

Estimations as to the effects of the general climatic trends of the Early Holocene on the Southern Argolid and the resultant malariogenic capacity are dependent on a consideration of the modern climatic conditions of the region and the influence of the topography on climatic patterns. Instrumental data from Nauplion (figure 3.5), lying 33 km to the northwest of Franchthi Cave, indicate a general pattern of mild, wet winters and hot, dry summers. Average temperatures range between 27.5˚C (July/August) and 10 ˚C (January); climatic studies show that summer temperatures rarely exceed 35˚C in the coastal regions of Greece, indicating ideal conditions for gonotrophic and sporogonic cycles (see chapter two) (Darby 1944). Winter temperatures rarely fall below 10˚C and frost is rare; snow fall occasionally occurs at elevations over 300 m, however the mild temperatures rarely permit snow to remain on the ground (Jameson *et al.* 1994)

Moisture availability decreases from the west to the east coast of the Southern Argolid; the eastern region is particularly arid due to the main mountain ranges, which, being oriented north-south, prevent a high percentage of precipitation from reaching the east coast (Darby 1944). Franchthi Cave, lying on the western extremity of the Franchthi headland, is therefore within a wetter area of the region. General monthly rainfall values vary from 4.3 mm in the

height of summer to above 92 mm in mid-winter, with an average of 500 mm per annum. The spatial distribution of annual rainfall levels vary considerably within the region. Gavrielides (1976) reports that “part of the [Franchthi headland] would receive a shower while [another] would remain completely dry”, despite being no more than 3-4 km apart; periodic droughts are a problem in the area, often with sequential years of low rainfall (cited in Hansen 1991:1,5; Darby 1944).

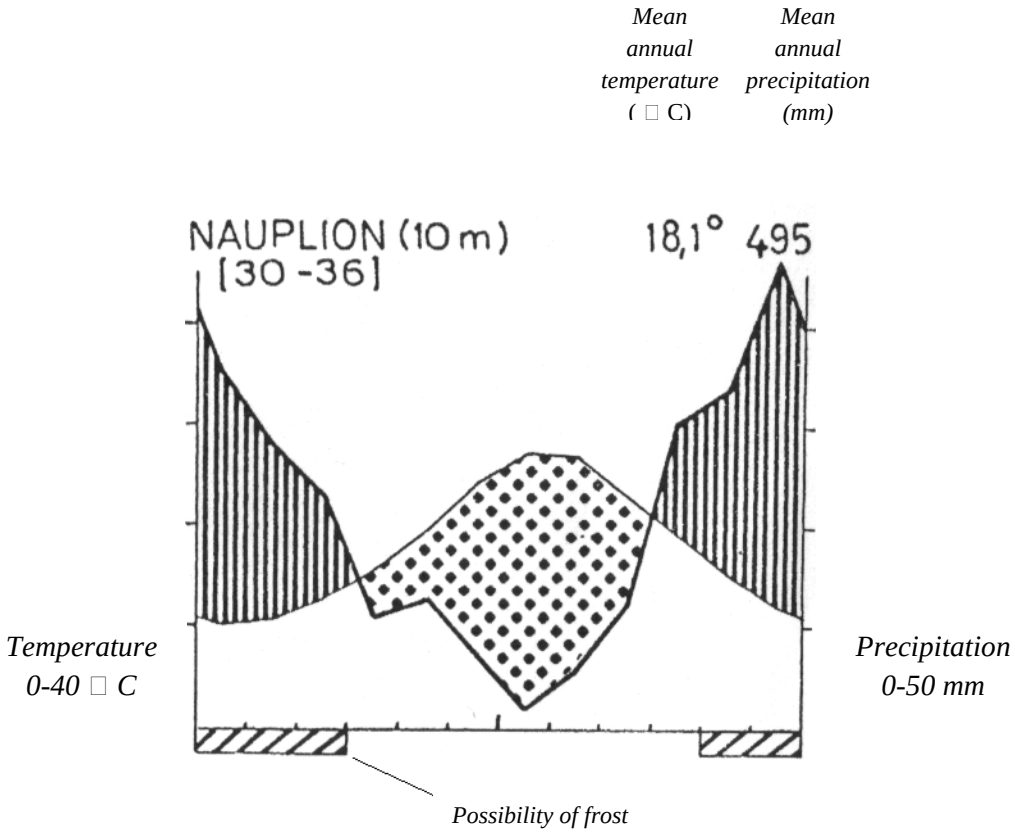


Fig 3.5: Climatic diagram of Nauplion, Argive Plain

Key: Vertical stripes indicate precipitation levels, white indicates temperature. Dots indicate overlap (*After* Walter *et al.* 1967: graph 115). *Italics* and key added by author.

Wind patterns exert a strong influence on rainfall over the Southern Argolid; the Asiatic anticyclone brings cool, arid winds from the north/north-east while the Atlantic anticyclone generates warm, wet winds from the south/south-west (Poulos *et al.* 1997). Wind patterns are extremely influential on malarial infection rates, especially on coastal sites, as the slightest breeze can interrupt mosquito flight while strong winds would completely hinder mosquito

activity in outdoor contexts. Studies indicate, however, that shelter would be sought by the vectors in such unfavourable circumstances, making indoor transmission more likely (Lividas *et al.* 1941). Historical texts, such as Theophrastus' *De Ventis*, permit wind patterns to be traced back to the 4th Century BC and, combined with knowledge of modern wind systems, may help reconstruct possible wind patterns of the past. Sea breezes are fairly constant throughout the year and stronger patterns emerge depending upon the season. South-westerlies predominate during the spring, while from May to October the Etesian winds prevail, a strong dry and cooling northerly wind system which can develop into gale force strengths. Autumn months are often affected by light westerly or southerly winds (*De Ventis* 38), while strong, cold and dry northerlies prevail across the Aegean during the winter months (Poulos *et al.* 1997). These patterns are, of course, not necessarily representative of the prehistoric periods, but do serve to illustrate that any malariogenic potential of the area would be somewhat restricted through exposure to the elements.

The effects of the climatic conditions between the Younger Dryas and the end of the Mesolithic within the Southern Argolid (summarised in figure 3.6) are hard to determine as proxy data sources from the region are unfortunately limited. There are no contemporary terrestrial pollen cores in the area, however pollen data is available from marine core C-40, (figure 3.3) the catchment area of which is suggested to be local rather than regional (Geraga *et al.* 2000). This theory is based on the inconsistency between this and other pollen cores from the eastern Mediterranean and boarder lands (Bottema 1974; Rossignol-Strick *et al.* 1992; Willis 1992a,b). Geraga (*et al.* 2000) suggest that the high frequency of arboreal pollen as opposed to semi-desert and steppe taxa in the marine core during the Palaeolithic period most likely reflects the well-watered locality along the Franchthi headland of the Southern Argolid (Geraga *et al.* 2000). Data from this core is therefore used to reconstruct the environmental and climatic conditions of the Franchthi headland within this thesis.

The widespread phenomenon of glacial conditions and intense aridity of the Aegean during the Younger Dryas would undoubtedly indicate that the tropical *Anopheles* vectors and *Plasmodiae falciparum* would have been precluded from the region; despite some indications of seasonal fluctuations, the pronounced cooling and aridity of the Aegean was unquestionably non-conducive for the completion of development and sporogonic cycles of the more virulent *Plasmodiae* (Denton *et al.* 2005). The suggested mean annual SST of c. 17 ˚C would however indicate that *P. vivax* and *P. malariae*, which are more tolerant of colder conditions, may have prevailed, carried by the autochthonous Mediterranean vectors (de Zulueta 1994; Gougou *et al.* 2007). Although transmission seasons would have been limited and the completion of the sporogonic cycle would have been slow, seasonal transmission would be possible under such temperatures. It is therefore suggested that these strains of malaria may have existed in the Southern Argolid prior to the Mesolithic settlement of Franchthi Cave; however the successful introduction of *P. falciparum* must have post-dated the termination of the Younger Dryas.

It is suggested that the increasing temperatures and precipitation levels following the termination of the Younger Dryas would have increased the malariogenic capacity of the Aegean; the abrupt increase in temperatures and augmented precipitation levels after c. 9050/8550 cal. BC (11000/10500 cal. BP)[36] would have rapidly created highly favourable conditions for both the tropical malarial vectors and parasites within the Southern Argolid. The natural aridity of the region is not suggested, based on the proxy data outlined above, to have been pronounced during the early Holocene. The presence of moisture-loving trees in core C-40 and the sedimentological evidence for precipitation levels three to four times those

[36] 9560±21 ^{14}C yr BP - 9283±17 ^{14}C yr BP (Reimer *et al.* 2004)

of the present day (van Andel *et al.* 1980; Hansen 1991; Geraga *et al.* 2000), would suggest that rainfall distribution was considerable, although perhaps muted in comparison with the excessively high values in the northern regions of Greece. Coastal areas are furthermore exposed to greater humidity levels than inland regions; the humidity levels in the Southern Argolid range from 60% to 100 % during the summer and heavy dew fall is common (Jameson *et al.* 1994), suggesting high water availability (Macdonald 1957; Tian *et al.* 2008).

Specific temperatures during the summer months cannot be reconstructed from the palaeoclimatic data; however the mean annual SSTs of c. 22 ˚C would indicate that the temperatures would have undoubtedly supported the malaria cycle during certain seasons, representing the optimum climatic range for both vector and parasite (Garnham 1964; Gougou *et al.* 2007). These warmer temperatures, combined with the trend of elevated humidity and precipitation levels, would indicate a potential for rapid vector development, extended longevity and a decrease in the duration of sporogonic cycles. Biting habits and vector life spans would also be increased, while the increased volumes of surface water, as indicated by elevated river discharges, would indicate a strong potential for high mosquito population density (Clements 1964; Leishout *et al.* 2004).

The significant reduction in seasonal variance during this period may potentially have permitted extended transmission seasons. The 5 ˚C increase in during the early Holocene to a mean annual temperature of 22˚C, with a *minimum* winter temperature of 16˚C in the southern Aegean Sea, indicates a muted seasonality, which may have resulted in longer transmission seasons and, by inference, a potential for high and prolonged exposure to the disease (Lividas *et al.* 1941; Gougou *et al.* 2007). During the 1930s, when malaria was rife within Greece, transmission was halted in the early winter months as temperatures dropped below 13 ˚C in the south; milder winters (14 ˚C and above) resulted in extended transmission

seasons and increased the potential for virulent epidemic-endemic cycles (Balfour 1935; Lividas *et al.* 1941).

Winter conditions as indicated by the southern Aegean SSTs were therefore at the threshold of *Plasmodium malariae* and *P. vivax* development (15˚C-16˚C) and infection from these plasmodia could have continued into the cooler months. The length of the sporogonic cycle would be at its longest, taking approximately 20 days to complete; the successful transmission of the parasite, or likelihood of infection, would therefore be minimal but plausible during the winter months (Garnham 1964). The presence of *P. falciparum*, requiring a minimum of 18˚C (Garnham 1964) or 19 ˚ C (Bruce-Chwatt *et al.* 1980) for sporogony to occur, is less plausible during the cooler seasons.

The success of winter transmission for all three *Plasmodiae* may, however, have been augmented by endophilic vector hosts. It has been noted that human dwellings or animal shelters, the favoured resting places of *A. sacharovi, A. superpictus* and *A. maculipennis* can produce temperatures 3 ˚C higher than the external temperatures (Garnham 1948); this would indicate minimum temperatures of 19˚C or above for hibernating mosquitoes, sufficient to allow sporogony of all three plasmodia to develop outside the usual seasonal parameters (Garnham 1948). At 20˚C or above, *P. vivax* and *P. malariae* would become a more significant risk for infection, as the cycle would shorten to 16 days. The minimum temperature required for *P. falciparum* (18˚C-19˚C) could also, within indoor environments, be attained, although the duration of the sporogonic cycle would be considerable at this temperature, taking approximately 20 days to complete (Garnham 1964). *Anopheles* vectors could undoubtedly remain active under such temperatures and though the conditions would suggest that the success of the gonotrophic and sporogonic cycles would have been at their slightest, infection could potentially have occurred during the coolest season of the year.

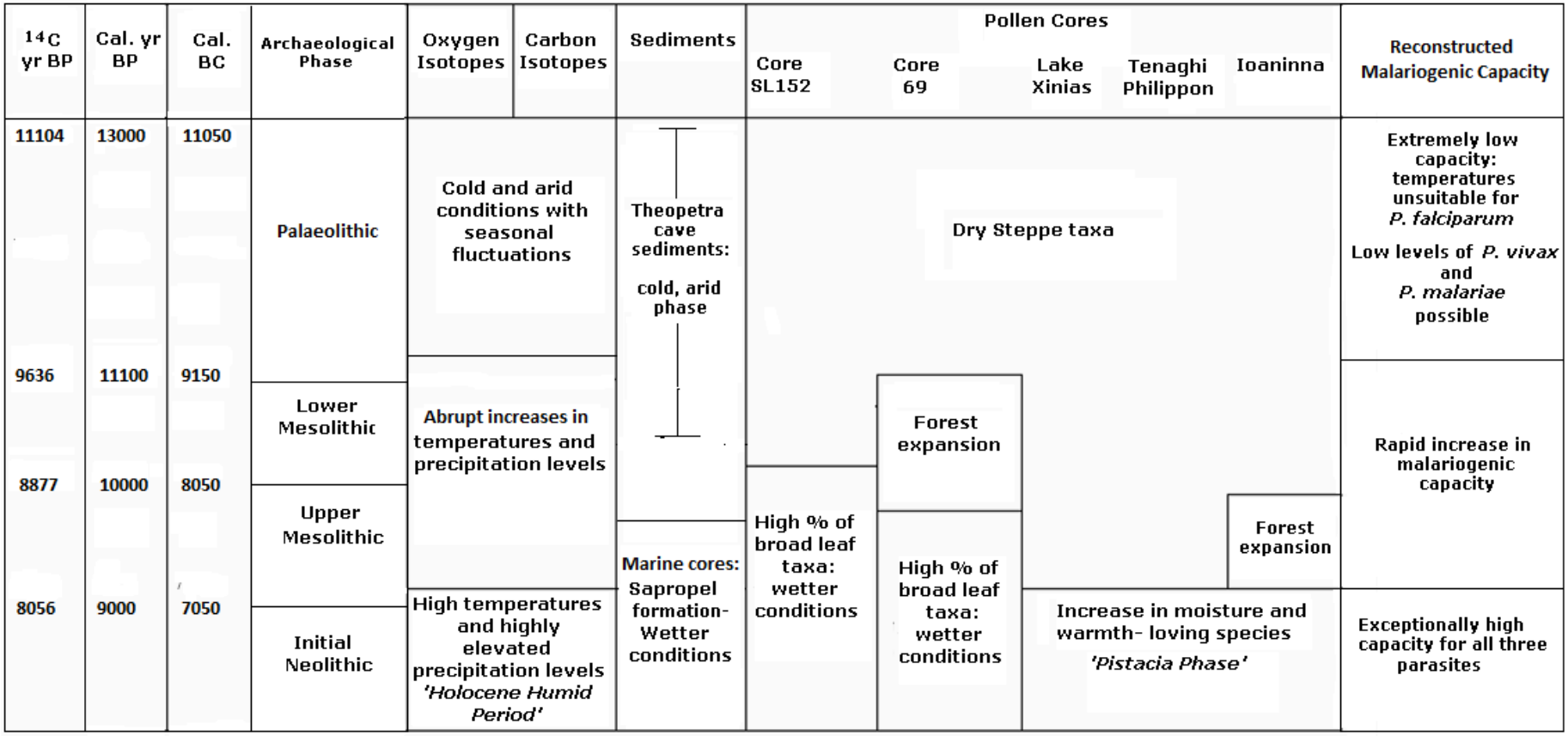


Fig. 3.6. Summary of palaeoclimatic trends and suggested malariogenic capacity of the Greek Mainland: 11500-7050 cal. BC (13000-9000 cal. BP).

Extended transmission seasons were therefore possible; a situation which in modern malarial studies have been linked to high infection rates and occasionally virulent epidemics (Balfour 1935; Barber *et al.* 1936; Lindsay *et al.* 1996).

The general climatic trend of the Mesolithic period after the limitations of the pronounced cooling of the winter temperatures during the Younger Dryas would therefore appear ideal for malaria transmission and the proxy data in fact indicate a greater capacity for malaria than that of Greece in modern history. The warming temperatures, high humidity and elevated precipitation levels are all factors which can constitute many of the requirements for endemic malaria (Macdonald 1957). The climatic warming of the early Holocene could therefore have supported a geographical expansion of the tropical vectors out of Africa and the Near East and into the Aegean; as mosquitoes colonise favourable habitats extremely rapidly, it is suggested that the introduction of the disease and *Plasmodiae* could have occurred soon after the climatic amelioration (Leishout *et al*. 2004; Zhou *et al*. 2004). Once introduced, the warmer, more humid climatic conditions and the subsequent muted seasonality would favour shortened reproduction and development rates, extended adult vector life spans, and increased biting behaviour.

The climatic information suggests, most importantly, that conditions appear to have been viable for not just *P. vivax* and *P. malariae* but also *P. falciparum,* particularly in southern Greece where temperatures were high. The climatic data would therefore broadly support Angel's (1969a; 1972) theory; it is concluded that a genetic immunity to malaria could not have developed within the Aegean prior to the Mesolithic, as the climatic conditions of the Younger Dryas would have precluded endemic malaria. The available climatic data would, however, indicate no climatic reason for *P. falciparum* and the tropical vectors to have been

excluded from the Aegean following c. 8550 cal. BC (10500 cal. BP)[37]. The success of an introduction at this point in prehistory with regards to environment and population density at Franchthi Cave will be debated in chapter four.

The Initial to Middle Neolithic (c. 7000-5300 cal. BC/ 8950-7250 cal. BP)

The favourable climatic conditions of the Mesolithic period continued into the Neolithic period (figure 3.2a-b). Planktonic foraminifera analyses from core LC21 indicates that high SSTs were sustained for approximately five centuries after c. 7550/7050 cal. BC (c. 9500/9000 cal. BP)[38], with a minimum winter temperature of 16 ˚C in the southern Aegean (figure 3.4) (Rohling *et al.* 2002). A comparison of fossil pollen data from core SL158 with modern pollen distributions indicate that climatic conditions in the northern Aegean region were equally stable, maintaining a mean winter temperature of c. 6 ˚C until c. 6850/6650 cal. BC (8800/8600 cal. BP)[39] (Kotthoff *et al.* 2008a). The latter study indicates that the high rainfall levels also persisted; winter precipitation levels remained above c. 275 mm and occasionally reached over 300 mm (Kotthoff *et al.* 2008a).

These highly conducive conditions began to deteriorate after c. 6850/6650 cal. BC (8800/8600 cal. BP); various sources of proxy data, including foraminifera analysis, $\delta^{18}O$ values from marine sediments and speleothems indicate a decline in temperatures and humidity levels, culminating three centuries later (c. 6250 cal. BC) in a dramatic climate change, termed the 8.2 ka BP event[40] (Bar-Matthews *et al.* 1999; Rohling *et al.* 2002; Gougou *et al.* 2007; Kotthoff *et al.* 2008a,b). This severe climatic downturn occurred in response to the final deglaciation of the Laurentide ice sheet; the release of the glacial water

[37] 9283±17 ^{14}C yr BP (Reimer *et al.* 2004)
[38] 8056±13 ^{14}C yr BP (Reimer *et al*. 2004)
[39] 7986±17 ^{14}C yr BP-7840±15 ^{14}C yr BP (Reimer *et al.* 2004)
[40] Commonly dated to 7400/7500 ^{14}C yr BP (Alley *et al.* 1997; Weninger *et al.* 2006). Northern marine core SL152 revealing a date of 7805±40 ^{14}C yr BP (reservoir correction of 400 years) (Kotthoff *et al.* 2008a).

caused a reduction in the northward heat transportation, resulting in a dramatic cooling of North Atlantic sea surface temperatures (Alley *et al.* 1997). This caused pronounced winter cooling on a global scale and the event is considered one of the most dramatic climatic deteriorations of the Holocene, representing over half the amplitude of the cooling during the Younger Dryas (O'Brien *et al.* 1995; Alley *et al.* 1997; Gasse *et al.* 2000; Rohling *et al.* 2002; 2005; Weninger *et al.* 2006).

Winter SSTs in the Aegean region decreased sharply by c. 2-4 ˚C (Geraga *et al.* 2000; 2005; Rohling *et al.* 2002). UK-37 analysis on core MNB-3 indicates that mean annual temperatures of the northern regions decreased by 3 ˚C to 19 ˚C. Foraminifera analysis from core LC21 indicate that winter SSTs decreased to c. 12-14 ˚C (figure 3.4) (Rohling *et al.* 2002); while winter temperatures in northern Greece, based on modern analogue functions of pollen cores from marine cores SL148 and SL152, are suggested to have decreased by 2 ˚C to c. 4 ˚C (Gougou *et al.* 2007; Kotthoff *et al.* 2008a,b). The 8.2 ka BP event was also marked with increased aridity; analysis of $\delta^{18}O$ values and sedimentological studies from marine cores in both the northern (SL148, SL152 and MNB-3) and southern Aegean Sea (LC21) indicate an interruption in the formation of sapropel 1, reflecting a decrease in humidity and precipitation levels which persisted for approximately two hundred years (Rohling *et al.* 2002; Kuhnt *et al.* 2007; Gougou *et al.* 2007; Kotthoff *et al.* 2008b). This phase of aridity and cooling is strongly reflected in pollen cores from both the southern marine core C-40 and the northerly cores SL148 and SL152, which indicate a gradual decrease in moisture-loving and frost-intolerant trees, such as *Tilia*, which nearly disappear from the record by 6050 cal. BC (8000 cal. BP)[41] in favour of dry taxa such as *Pinus* and *Artemisia* (Geraga *et al.* 2005; Kuhnt *et al.* 2007; Kotthoff *et al.* 2008a,b).

[41] 7187±19 ^{14}C yr BP (Reimer *et al.* 2004)

It has been suggested that, as with the Younger Dryas, the cooling and aridity was a seasonal phenomenon in some regions, predominantly affecting the winter months (Bar-Matthews *et al.* 1999; Gasse 2000; Frisia *et al.* 2006; Weninger *et al.* 2006). The continued, although reduced, presence of *Tilia* in these pollen cores indicates that the spring and summer precipitation levels were less affected (Rossignol-Strick 1995); this is supported by the application of MAT to pollen assemblages from cores SL148 and SL158, which indicates that precipitation levels in the northern regions of the Aegean remained elevated in comparison to the modern values, barely decreasing below 300 mm (Kotthoff *et al.* 2008a,b). The seasonal aridity would therefore appear to have been relative to the high humidity levels of the Early Holocene and conditions in the north remained wetter than those of the modern.

Regional proxy data indicate that the pronounced cooling of the 8.2 ka BP event persisted until c. 5950 cal. BC (7900 cal. BP)[42], when SSTs within the Aegean began to increase. Foraminifera analysis from LC21 in the southern Aegean sea indicates that SSTs reached a minimum of 16 ˚C by c. 5850 cal. BC (c. 7800 cal. BP) (figure 3.4), while UK-37 analysis from core MNB-3 indicate an annual mean SST of 23 ˚C, the highest recorded value during the deposition of sapropel 1 (Gougou *et al.* 2007). The application of MAT to marine pollen cores from cores SL148 and SL158 indicate a contemporary increase in winter temperatures to c. 6 ˚C and in winter precipitation levels, which increased to c. 300 mm; this is supported by $\delta^{18}O$ values from LC21, which indicate that precipitation and humidity levels remained elevated until c. 5550 cal. BC (7500 cal. BP)[43] (Rohling *et al.* 2002; Kotthoff *et al.* 2008 a, b; Gougou *et al.* 2007; Kuhnt *et al.* 2008).

This climatic pattern is not reflected in local proxy data from central and southern Greece, which indicate that the aridity associated with the 8.2 ka yr. BP event may have persisted into

[42] 7034±15 ^{14}C yr BP (Reimer *et al.* 2004)
[43] 6610±17 ^{14}C yr BP (Reimer *et al.* 2004)

the Middle Neolithic. Sediment studies from Theopetra Cave have identified a major erosional event between 5926 and 5787 cal. BC (7875-7736 cal. BP)[44] (Karkanas 2001), an event which Karkanas (2001) suggests is broadly contemporary with a stratigraphic gap at Franchthi Cave between c. 6550-6050 BC (c. 8500-8000 BP) (Farrand 2000); both, he suggests, may be linked to the intense cooling and increasing aridity of this period. It is also possible that these events were linked to anthropogenic influence upon the local environment, or that the local karst[45] systems were responsible for these erosional events (Farrand 1988; Karkanas 2001). The theory of an extended period of aridity is, however, supported by pollen records from Kiladha Bay in the Southern Argolid, which reflect an extremely dry climate between c. 5765 and 5536 cal. BC (7714-7485 cal. BP)[46]. Data indicate an open steppe-like environment with hot, dry taxa, such as *Ephedra* and *Artemisia,* suggesting low precipitation and water availability; open oak forests grew at higher altitudes while other deciduous tree species became rarer, and are most likely to have grown in highly localised sites along water courses (Bottema 1990). It must be noted that this alteration in taxa may also have been influenced by anthropogenic activity of the Middle Neolithic. The veracity of these proxy sources as climatic indicators may therefore be questioned.

Other sources of proxy data from the Southern Argolid contradict the theory of increasing aridity, indicating that water availability persisted within the region. Evidence for a thick calcareous film encasing pottery sherds from Franchthi Cave dating to 5610 cal. BC (7559

[44] 7036±44 and 6911±32 ^{14}C yr BP (Karkanas 2001)
[45] Subterranean drainage systems ('katavothroi') formed through bedrock erosion. Theopetra and Franchthi form part of a karstic system (Farrand *et al.* 2000; Karkanas 2001).
[46] The Kiladha Bay core produced three radiocarbon dates; the last of these has too great a standard deviation to be accurate (Bottema 1990). Calibrated with OxCal 4.1 to σ2.

^{14}C yr BP	**Cal. BP**	**Cal. BC**	**Median cal. BC**
6860±120	7941-7509	5992-5560	5765
6720±100	7757-7428	5808-5479	5637
6600±250	7958-6960	6009-5011	5536

cal. BP)[47] have been interpreted as evidence of an "unusually wet period", where increased rainfall or water availability augmented the deposition rate of calcareous deposits (Vitelli *et al*. 1999: 11). This is supported by seismic profiling studies on the buried Franchthi river in Kiladha Bay, the enlarged cross-section of which indicates that the river remained extremely active until c. 5050-4050 BC (c. 7000-6000 BP); the authors of the study interpret the data as evidence of precipitation levels three times those of the modern (van Andel *et al*. 1980). While the dating of the latter study is not exact and these data sets may not therefore be contemporary, it is possible that these contradicting data sets reflect the highly variable spatial distribution of rainfall within the Southern Argolid as noted by Darby (1944) and Gavrielides (1976 in Hansen 1991), who reported that regions only 3-4 km apart would receive different volumes of rainfall. The pollen from the Kiladha core, deposited by aeolian and fluvial transport, may therefore reflect the arid conditions of the wider region, while the cave deposits and river sediments represent localised, wetter foci. This would support Bottema's (1990) theory of localised water sources, indicating that the streams and rivers in the region, and in the vicinity of Franchthi Cave, remained active within an overall climatic trend of increasing aridity.

$\delta^{18}O$ and $\delta^{13}C$ values from speleothems and fossil foraminifera from the Levant and Aegean would suggest the introduction of a more variable climatic regime after c. 5550 cal. BC (7500 cal. BP) which culminated in c. 5150 cal. BC (7100 cal. BP)[48], during the Late Neolithic period with a period of pronounced cooling and aridity (Bar-Matthews *et al.* 1999; Rohling *et al.* 2002; Kotthoff *et al.* 2008a,b). The nadir in temperatures and precipitation levels is evident in marine cores from the north Aegean Sea due to the termination of sapropel 1 (Kuhnt *et al.* 2007); although this sedimentological change is not evident in core MNB-3

[47] 6690±80 ^{14}C yr BP (Vitelli *et al.* 1999)
[48] 6610±17 ^{14}C yr BP and 6179±17 ^{14}C yr BP (Reimer *et al.* 2004)

until 4750 cal. BC (6700 cal. BP) and not until 4450 cal. BC (6400 cal. BP) [49] in the southern core, LC21; this event marks a weakening of the monsoon systems and an inexorable decline in moisture availability (Rohling *et al.* 2002; Gougou *et al.* 2007; Kotthoff *et al.* 2008a).

The climate and malariogenic capacity of the Neolithic climate

Franchthi Cave

Franchthi Cave was occupied throughout the Neolithic period, however the osteological evidence only extends to the Middle Neolithic Period; the climatic conditions and malariogenic capacity of the Late Neolithic are not therefore considered within this thesis (figure 3.2a) (Angel 1969a).

The elevated precipitation levels of the Aegean following the transition to the HHP (figure 3.7) were undoubtedly exceptionally favourable for *Anopheles* vectors and all three malarial *Plasmodiae*. The warmer conditions, muted seasonality and elevated humidity and precipitation patterns of this period, encompassing the Initial Neolithic and the beginning of the Early Neolithic, would appear to be ideal for the successful transmission of the disease. These general climatic trends indicate a high malariogenic capacity as the suggested mean annual temperature of 23 ˚C (Gougou *et al.* 2007) would have facilitated rapid reproduction rates and growth patterns, while the minimum winter temperatures of 16 ˚C in the southern Aegean (Rohling *et al.* 2002) would suggest a potential for extended transmission seasons, prolonging infection into the autumn and winter months. The elevated humidity and rainfall levels of the Initial Neolithic period in the Southern Argolid, supported by sediment analysis of buried river beds (van Andel *et al.* 1980), would furthermore suggest a capacity for long vector life-spans and a high availability of breeding grounds.

[49] 5892±17 ^{14}C yr BP and 5602±15 ^{14}C yr BP (Reimer *et al.* 2004; Gougou *et al.* 2007)

The sedimentary gap at Franchthi Cave between c. 6550-6050 BC (8500-8000 BP) is interpreted as evidence of an extended occupational hiatus of approximately 500 years, a contention which is supported by ceramic studies (Vitelli 1993). The cave was not, therefore, occupied for the majority of the 8.2 ka BP event[50]; however temperatures did not increase until c. 5950 cal. BC (7900 cal. BP)[51], suggesting that the reoccupation of the cave took place during the extended period of cold and arid conditions. The malariogenic capacity of the region would have been significantly lower than during previous periods, as vector lifespan, egg survival rates and transmission seasons would have been compromised by both the decreasing humidity levels, and the 2-4 ˚C decrease in temperature (Rohling *et al.* 2002; Kuhnt *et al.* 2007). As the climatic deterioration is suggested to have been restricted to the winter months, it is hypothesised that the malaria transmission would only have been possible during the warmer seasons, introducing a more unstable, seasonal malariogenic capacity.

The higher temperatures recorded following c. 5950 cal. BC (7900 cal. BP)[52], encompassing the Late Early Neolithic and the beginning of the Middle Neolithic period, would suggest that the potential for stable malarial transmission during the sixth Millennium BC was extremely high. The mean annual temperature of c. 23 ˚C and increased precipitation levels (Gougou *et al.* 2007) would suggest a high malariogenic capacity, capable of supporting rapid reproduction rates and sporogonic cycles of *P. falciparum,* as well as *P. vivax* and *P. malariae,* extended longevity and increased biting behaviour of the *Anopheline* vectors (Macdonald 1957).

Whether this climatic amelioration affected the Southern Argolid is however debatable, as local proxy data, such as the pollen core from Kiladha Bay may serve to indicate that the

[50] Commonly dated to 7400/7500 ^{14}C yr BP (Alley *et al.* 1997; Weninger *et al* 2006).
[51] 7034±15 ^{14}C yr BP (Reimer *et al.* 2004)
[52] 7034±15 ^{14}C yr BP (Reimer *et al.* 2004)

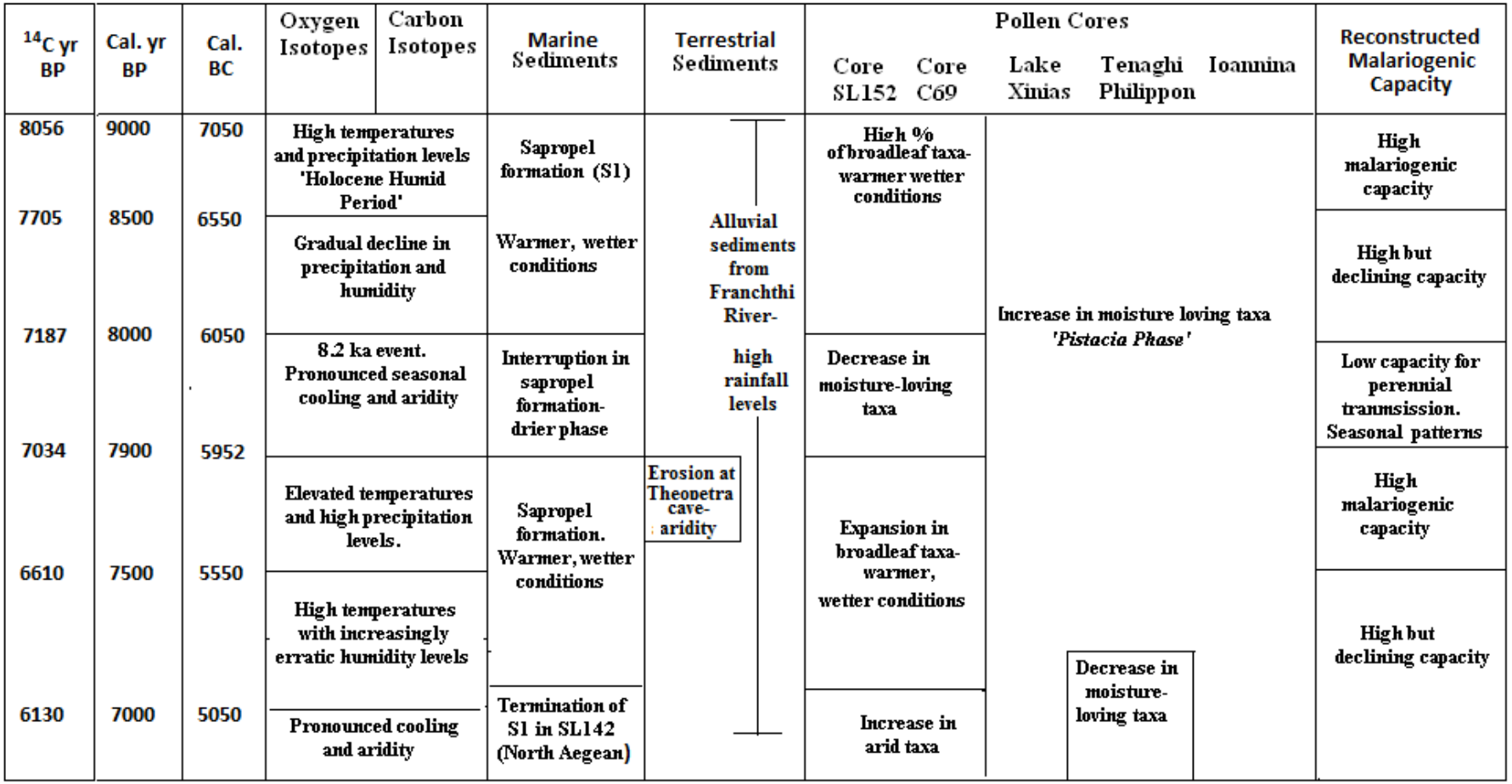


Fig. 3.7. Palaeoclimate and Malariogenic capacity of the Aegean: 7050-5050 cal. BC (9000-7000 cal. BP)

aridity of the 8.2 ka BP event persisted throughout the Early Neolithic (Bottema 1990). It is noted that the coastal positioning of Franchthi Cave may have mitigated the effects of the aridity; the minimum humidity level of 60% due to marine influences would protect vector populations against desiccation or reduced life spans. The lower precipitation levels over the southern Aegean may therefore have limited the spatial distribution of the vectors; but the humidity levels, combined with the presence of localised water sources across the region, may instead have created intense foci of vector populations, which modern studies suggest can result in highly augmented numbers of drought tolerant species (Macdonald 1957; Bouma *et al.* 1994a,b; Leishout *et al.* 2004). Combined with high temperatures, these conditions could have resulted in rapid sporogonic and gonotrophic cycles and extended transmission seasons, but only within certain locations capable of supporting vector oviposition, creating a more intensive or unstable malariogenic capacity.

The increasing aridity during the Middle Neolithic and specifically after c. 5500 cal. BC (7500 cal. BP)[53] (Bottema 1990; Rohling *et al.* 2002; Kotthoff *et al.* 2008a) would indicate an irrevocable change in the malariogenic capacity, as the highly conducive precipitation and humidity levels of the Early Holocene began to decline. This climatic deterioration is not suggested to have entirely curtailed transmission, although the longevity of the *Anopheline* vectors and distribution of breeding grounds may have been limited; it is suggested, however, to mark the beginning of a transition to a different climatic regime, leading to a nadir in temperatures and precipitation levels and the termination of sapropel 1 in the northern marine cores by c. 5050 cal. BC (c. 7100 cal. BP)[54], an event which marks an inexorable decline in moisture availability (Rohling *et al.* 2002; Gougou *et al.* 2007; Kotthoff *et al.* 2008a).

[53] 6610±17 ^{14}C yr BP (Reimer *et al.* 2004)
[54] 6179±17 ^{14}C yr BP (Reimer *et al.* 2004)

Although the osteological evidence at Franchthi does not extend to the Late Neolithic and this chronological period is therefore outside the scope of this thesis; the climatic change within this period is important with regards to subsequent malariogenic capacity, as the decline in precipitation and humidity would signal a significant alteration to the potential longevity of *Anopheline* vectors and in the abundance of breeding grounds.

Nea Nikomedeia

Nea Nikomedeia, sited on the Veria Plain in northern Greece, is suggested to have been settled just prior to the 8.2 ka cal. BP[55] event and was occupied until the end of the Early Neolithic period (figure 3.2b) (Perlès 2001; Weninger *et al.* 2006). Two radiocarbon dating samples indicate a later phase of occupation, which, in conjunction with archaeological evidence, suggest a reoccupation of the site during the Late Neolithic, following an extended occupational hiatus (Rodden *et al.* 1996). The osteological evidence from Nea Nikomedeia pertains, however, to the Early Neolithic and it is only this phase that is considered within this thesis.

Modern climatic trends of the Veria Plain, taken from climatic stations at Thessaloniki (figure 3.8), would indicate that this region, having a far wetter climate than that of the more arid Southern Argolid, may have retained a higher malariogenic capacity during the arid event at 8.2 ka cal. BP than the southerly regions of Greece. Summers are dry and warm with temperatures reaching c. 26-28 ˚C and winters are wet and mild with an average December /January temperature of c. 6-7 ˚C (Meteorological Office 1915; Ivanova *et al.* 2002).

[55] Commonly dated to 7400/7500 14C yr BP (Alley et al. 1997; Weninger et al 2006).

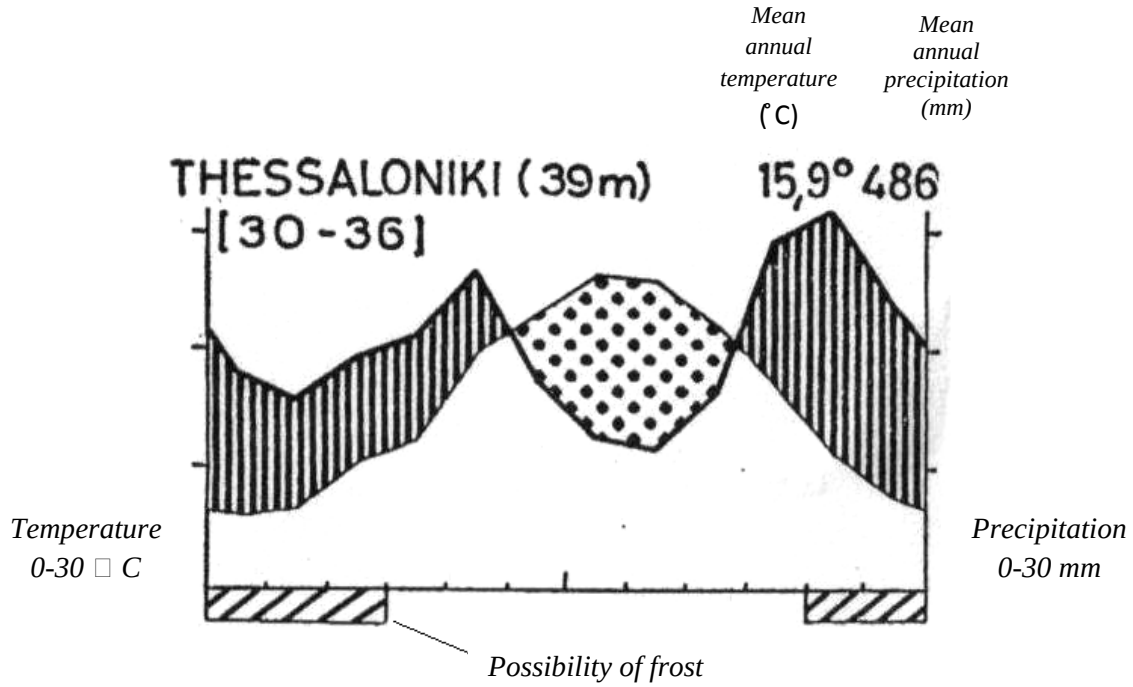


Fig. 3.8. Climatic diagram from Thessaloniki, Northern Greece

Key: Vertical stripes indicate precipitation levels, white indicates temperature. Dots indicate overlap. (*After* Walter *et al.* 1967; graph 118). *Italics by author.*

The distribution of annual rainfall across the plain is largely determined by the topography. The Pindus Mountains create a vast rainfall shadow effect towards the east of the mainland, causing rainfall levels to decrease gradually from the west to the east. The area surrounding Nea Nikomedeia receives higher levels of rainfall in comparison with other areas of the plain, including the city of Thessaloniki, as the site lies at the foothills of the Vermion Mountains which receive an average of 800 mm per annum. The malariogenic capacity of the eastern area of the plain of Veria would therefore potentially be appreciatively higher than in the central and eastern part of the plain, as precipitation levels diminish progressively towards the east to an average of 400 mm per annum (Bottema 1974). Annual precipitation levels vary considerably; climatic studies show significant variations in rainfall levels in the region of Thessaloniki with winter, the wettest season of the year, receiving as little as c. 37 mm some

years and as much as c. 285 mm in others, the latter representing the highest recorded level between 1898 and 1984 (Kutiel *et al.* 1996; Xoplaiki *et al.* 2000).

Wind patterns in the area have a marked effect on temperatures and humidity levels; however it is notoriously difficult to project this climatic parameter into the past with any certainty. Modern wind patterns, combined with the wind patterns recorded by Aristotle in *Meteorologica* in the late fourth century BC, although not accurate portrayals of those of the Neolithic, do serve to illustrate the potential weather patterns which would have affected the distribution of any mosquito populations. The coastal area is subject to sea breezes on a perennial basis, while the spring and summer months experience the north-eastern Etesian winds which blow from May to October and can gain some strength (*Meteorologica* 361b35-362a2; Poulos *et al.* 1997). Cold dry polar winds, known as the Vardar winds, blow from the north along the Axios river valley causing temperatures to plummet by as much as 10°C along the central plain during the winter and spring (Bottema 1974; Poulos *et al.* 1997); strong northerly winds were also noted by Aristotle (*Meteorologica* 364a32-364b3). A strong Etesian or Vardar wind would undoubtedly temper mosquito activity considerably as a temperature decrease of this magnitude will kill or force the vector to hibernate, limiting or terminating its biting activity. The risk of endophagic behaviour and therefore of infection rates is, however, increased by such conditions (Lividas *et al.* 1941).

The settlement of Nea Nikomedeia is suggested to have been established during the gradual climatic deterioration after c. 6850/6650 cal. BC (8800/8600 cal. BP)[56] as temperatures and humidity levels declined. Data from marine core SL152 (figure 3.3) are suggested to predominantly reflect the conditions of northern Greece rather than those of Asia Minor and northern Turkey due to the higher sediment influx from the rivers of northern Greece, with

[56] 7986±17 ^{14}C yr BP – 7840±15 ^{14}C yr BP (Reimer *et al.* 2004)

the Axios contributing the second largest sediment influx, after the Evros River (Kotthoff *et al.* 2008a). Data from this core indicate that the precipitation levels of the northern region, although lowered from previous periods, remained higher than those of the modern, as levels approached c. 270 mm (Kotthoff *et al.* 2008). Malaria studies in Macedonia during the 1930s linked rainfall levels of c. 200-220 mm to an increased abundance of *Anopheles* vectors, as the volume of surface water and therefore of potential breeding grounds, increased exponentially (Barber *et al.* 1936; Kutiel *et al.* 1996). The suggested mean annual temperature (although gradually declining) of c. 23 ˚C (Gougou *et al.* 2007), would indicate that such wet seasons may logically be linked to a considerable malariogenic capacity during the spring and early summer.

The abrupt decrease in winter temperatures in c. 6250 cal. BC (8200 cal. BP) would have undoubtedly limited the malariogenic capacity, preventing extended transmission seasons. This decrease is suggested to have affected the northern regions of Greece more markedly than the southern; the 2˚C decrease in mean winter temperatures to c. 4 ˚C (Kot thoff *et al.* 2008a) as opposed to 12˚C -14 ˚C in the southern Aegean Sea (Rohling *et al.* 2002) would undoubtedly have terminated malaria transmission during the early winter or perhaps the late autumn. The development cycles of the *Anopheles* vector and the sporogonic cycle of the *Plasmodiae* could not be completed under such temperatures, while vectors would either die or become torpid under such conditions (Macdonald 1957).

The suggestion that this decrease in temperature was a seasonal event, affecting only the winter temperatures (Bar-Matthews *et al.* 1999; Gasse 2000; Frisia *et al.* 2006; Weninger *et al.* 2006; Kotthoff *et al.* 2008a) would imply that the spring to autumn months may have remained conducive to both the vector and the *Plasmodiae.* This contention is supported by the evidence for high precipitation levels of the northern Aegean regions (Kotthoff *et al.*

2008a); the malaria transmission season may therefore have been shorter in comparison with those of the southern Aegean due to lower temperatures, but the higher water availability of the northern regions are likely to have increased vector populations, suggesting a high malariogenic capacity during the spring and summer months. Seasonal or unstable transmission may therefore be considered plausible in both northern and southern regions during this period despite different climatic trends.

The subsequent period of higher temperatures and wetter conditions recorded for the period of c. 5950 - c. 5550 cal. BC (7900 cal. BP to 7500 cal. BP)[57], would indicate an increased malariogenic capacity. The mean annual temperature of c. 23 ˚C would support rapid reproduction rates and biting behaviour; although the suggested winter temperatures of 5-6 ˚C (Kotthoff *et al.* 2008a) would indicate that malarial transmission would have been halted during the autumn months. The reconstructed precipitation levels of this period, suggested to have been elevated to c. 300 mm, would, however, represent unprecedented levels in comparison to instrumental data for winter rainfall levels for Thessaloniki between 1892 and 1991 AD; the wettest winters during this century are recorded to have reached 285.4 mm between 1935 and 1936 which, in conjunction with average summer temperatures of c. 26 ˚C were noted to result in a year of exceptional infection rates (Lividas *et al.* 1941; Xoplaiki *et al.* 2000; Kotthoff *et al.* 2008a). The heavy rainfall patterns resulted in expanded breeding grounds and increased longevity of the *Anopheline* vectors, causing severe epidemics across northern Greece that persisted throughout the drier months (Balfour 1935; Barber *et al.* 1936; Lividas *et al.* 1941). The phenomenon has been noted in global malaria studies and is largely due to the notorious speed at which *Anopheles* vectors will colonise areas of surface water once heavy rainfall has ceased and the consequential explosions in vector populations

[57] 7034±15 ^{14}C yr BP - 6610 ± 17 ^{14}C yr BP (Reimer *et al.* 2004)

(Bouma *et al.* 1994a,b). These projected precipitation patterns from core SL152, combined with the higher mean temperatures, would therefore suggest an exceptionally high climatic malariogenic capacity for the end of the Early Neolithic period and the end of the initial occupation phase of Nea Nikomedeia.

The proxy data from the Aegean would appear to broadly reflect an increasing malariogenic capacity during the Initial and Early Neolithic and a subsequent decline during the Middle Neolithic, which would support Angel's (1969a; 1971; 1972) theory. The potential for perennial transmission is suggested to have been almost continual in the southern regions during the apparently highly stable climatic conditions of the Mesolithic and Early Neolithic, while the north of Greece is suggested to have been subject to a more epidemic-endemic cycle due to the colder winter temperatures. The transition to a more arid climate during the late Early Neolithic to the early Middle Neolithic, limiting water availability and humidity levels, is suggested to have reduced the malariogenic capacity in both the northern and southern regions, potentially resulting in unstable transmission patterns.

The Bronze Age (3300-1100 cal. BC/ 5150-3050 cal. BP)

The Bronze Age began with an increase in temperatures, as proxy data from both southern and northern cores indicate that the mean annual temperatures had once again increased to equal those of the modern (Geraga *et al.* 2005; Gougou *et al.* 2007). The most significant alteration was to humidity levels, which progressively decreased throughout the Late Neolithic, culminating in the cessation of the 5000 year long Holocene Humid Period. The extremely abrupt termination of this phase is dated by the termination of sapropel 1 to c. 4450 cal. BC (6400 cal. BP)[58] in LC21 in the southern Aegean and to c. 3550 cal. BC (5500 cal.

[58] 5892±17 ^{14}C yr BP (Reimer *et al.* 2004)

BP)[59] in core C69 (figure 3.4) (Rohling *et al.* 2002; Geraga *et al.* 2005). The termination of sapropel 1 indicates the cessation of the high precipitation values; $\delta^{18}O$ and $\delta^{13}C$ values from all Aegean marine cores and speleothems from the Levant indicate that summer evaporation increased globally during the transition to the Bronze Age (Bar-Matthews *et al.* 1997; 1999; deMenocal *et al.* 2000; Geraga *et al.* 2000; Bond *et al.* 2001; Rohling *et al.* 2002; Sangiorgi *et al.* 2003). This event is not synchronous within the eastern Mediterranean; while marine cores in Africa date this event to 3550 cal. BC (5500 cal. BP)[60] (deMenocal *et al.* 2000; Artz *et al.* 2003), the termination of sapropel 1 appears to have occurred far earlier in the northern regions of Greece. Deposition ends in core SL142 in c. 5150 cal. BC (c. 7100 cal. BP)[61] and in c. 4750 cal. BC (6700 cal. BP)[62] in core MNB-3 (Gougou *et al.* 2007; Kuhnt *et al.* 2007). Each core, however, indicates that the transition out of the HHP was abrupt, occurring within a century or less.

Temperatures appear to have remained high, as foraminifera analysis from both southern and northern cores indicate that winter SSTs reached a minimum of 16 ˚C and 6 ˚C respectively and appear to have remained stable for approximately four centuries; precipitation levels continued to decline as the millennia progressed, gradually becoming more akin to the sharply delineated rainfall patterns of the modern Aegean (Rohling *et al.* 2002; Kotthoff *et al.* 2008b). $\delta^{18}O$ values from planktonic and benthic foraminifera in marine cores LC21, C69, SL152 and SL148 across the Aegean indicate a predominance of near-drought conditions between c. 3000 and c. 2500 BC (4950 and 4450 cal. BP)[63] (figure 3.4), as summer evaporation and winter temperatures increased (Geraga *et al.* 2000; Rohling *et al.* 2002; Kotthoff *et al.* 2008a). Reconstructed precipitation levels from the Thermaic Gulf, based on

[59] 4793±13 ^{14}C yr BP (Gougou *et al.* 2007)
[60] 4590±40 ^{14}C yr BP (after 500 year reservoir correction) (DeMenocal *et al.* 2000)
[61] 6179±17 ^{14}C yr BP (Reimer *et al.* 2004)
[62] 5892±17 ^{14}C yr BP (Gougou *et al.* 2007)
[63] 4368±13 ^{14}C yr BP - 4032±12 ^{14}C yr BP (Reimer *et al.* 2004)

modern analogue functions of fossil pollen records, would however indicate that the arid conditions were not as pronounced in the northern region, as the mean winter rainfall levels are suggested to have remained at c. 300 mm (Kotthoff *et al.* 2008a).

The increasing aridity of the Early Bronze Age across the southern regions appears to have been punctuated by episodes of extreme climatic conditions. Episodes of flooding are evident in both palaeoclimatic data and archaeological evidence, which have been linked to widespread episodes of landscape instability across the Aegean, in Crete (Moody 2000), Attica (Paepe 1980) and on the Argive plain (Pope *et al.* 1984; Zangger 1993; 1994). These have been interpreted as a result of heavy rainfall, especially in the latter case, where Zangger (1993; 1994) suggests that the torrential floods or 'inundations' were sufficiently severe to have restricted habitation patterns during this period (1994: 201)[64]. This will considered further in chapter six.

Malaria transmission patterns would have changed drastically by 2200-2000 cal. BC (c. 4150-3950 cal. BP)[65]; $\delta^{18}O$ values from LC21 indicate that humidity levels decreased while the distribution of planktonic foraminifera would infer that winter temperatures remained extremely high (Rohling *et al.* 2002), resulting in a well-recognised drought phase across the Greek mainland which persisted for approximately 200 to 300 years (figure 3.4) (Rohling *et al.* 2002; Ehrmann *et al.* 2007; Kuhnt *et al.* 2007). This phase of intense aridity appears to have been a global phenomenon of almost catastrophic proportions and has been linked to widespread settlement destructions and abandonments in the Aegean (Weiss 2000), the Indus Valley (Staubwasser *et al.* 2003) and in areas of the Ancient Near East, such as in Northern Mesopotamia (Weiss 2000; Cullen 2001). A significant reduction in water availability is

[64] No radiocarbon dates are available for these episodes of soil instability, each having been dated through archaeological and ceramic evidence to EHII (see figure 3.9) (Paepe 1980; Zangger 1993; 1994; Moody 2000).
[65] 3777±13 ^{14}C yr BP – 3622±14 ^{14}C yr BP (Reimer *et al.* 2004)

noted in global proxy data: the Dead Sea water levels fell by an incredible c. 45 m in c. 2000 BC (c. 3950 BP) (Enzel *et al.* 2003), while historical records show that the annual Nile floods failed spectacularly, causing severe famine in Egypt (Bell 1975; Weiss 2000). Varved sediments from Lake Van in Turkey indicate a contemporary lowering of lake water levels and decrease in *Quercus* pollen, leading the authors to suggest a decreased spring rainfall (Wick *et al.* 2003).

The Middle Bronze Age began during this extended and extremely pronounced drought. Foraminifera analysis from core LC21 indicates that winter temperatures remained very high, approaching a minimum of 16°C; the humidity levels were, however, less conducive to malarial transmission, remaining far below the Holocene average (Rohling *et al.* 2002). $\delta^{18}O$ from the southern Aegean cores indicate that humidity and rainfall levels increased after c. 1750 cal. BC (3700 cal. BP)[66]; this increase is manifested in Cretan pollen cores which indicate a slow recovery in moisture availability as tree pollen had increased by c. 1750 BC (Moody *et al.* 1996; Rohling *et al.* 2002; Bottema *et al.* 2003; Moody 2005a,b). These climatic patterns are also reflected in $\delta^{18}O$ values from foraminifera assemblages in Africa, which indicate that temperatures remained high as summer evaporation levels declined in c. 1750 cal. BC (3700 cal. BP), reflecting a moister and milder climate (deMenocal *et al.* 2000; Rohling *et al.* 2002).

$\delta^{18}O$ values of foraminifera assemblages from core LC21 indicate that the beginning of the 17th century BC saw a continuation of warm temperatures and a minor decrease in summer evaporation levels (Rohling *et al.* 2002; Moody 2005). There are some indications that the climate became increasingly erratic; $\delta^{18}O$ values from speleothems indicate that rainfall levels fluctuated considerably in the Near East during this period (Bar-Matthews *et al.* 1997),

[66] 3459±15 ^{14}C yr BP (Reimer *et al.* 2004)

a phenomenon which appears to have been reflected in Egypt, where historical texts show intensive and repeated flooding episodes occurred between 1863 and 1764 BC (Bell 1975).

Proxy climatic data indicate widespread climatic anomalies during the second half of the century, which may have been due to, or at the very least exacerbated by, the volcanic eruption of Thera in c. 1627-1600 cal. BC (3687-3580 cal. BP)[67] (Freidrich *et al.* 2006). A re-estimation as to the volume of the eruption indicate that the eruption equated to a 6 or 7 on the volcanic explosivity index (VEI), indicating that the eruption was comparable to that of Tambora in 1815. Estimated to have produced 100 km^3 of tephra and a 36 km high plume, the dust from the Thera eruption could have passed into the stratosphere and therefore plausibly have altered global climatic patterns, in a similar manner to the Tambora eruption over two thousand years later (Sigurdsson *et al.* 2006). It has been suggested that the volume of sulphur-dioxide emissions from such an eruption would have resulted in several years of warmer winters and cooler summers in the Aegean area (Pyle 1997). This supposition is still debated as some scholars question the suggested extent of the environmental and climatic effects of this eruption (Eastwood *et al.* 2002); however, regardless of the provenance or potential causes, global proxy data clearly indicate broadly synchronous climatic anomalies which would have strongly affected malariogenic patterns.

The climatic changes suggested by Pyle (1997) are not visible within the oxygen isotope values or foraminifera distribution within the marine cores of the Aegean, perhaps due to the suggested brevity of such a climatic event which the sampling resolution of the cores cannot discern. Rather than an increase, analysis of planktonic foraminifera from core LC21 indicates a drop in winter SSTs following the volcanic eruption, while $\delta^{18}O$ values indicate a contemporary increase in moisture availability (figure 3.4) (Rohling *et al.* 2002). This colder

[67] Four dates of 3383±11, 3372±12; 3349±12 and 3331±10 ^{14}C yr BP were produced (Freidrich *et al.* 2006).

event appears to be reflected in global proxy data; isotopic evidence from Hungary and tree ring data from Ireland, Germany, Sweden and western USA indicate an abrupt cooling, indicating frost damage dating to the latter part of the 17th century BC (La Marche *et al.* 1984; Baillie *et al.* 1988; Grudd *et al.* 2000; Siklosy *et al.* 2009). $\delta^{18}O$ values from core GA110 and GA112 indicate a contemporary increase in humidity which is again supported by high Dead Sea levels (Frumkin *et al.* 1991; Schilman *et al.* 2001). Precipitation regimes appear to have been variable in some regions during this period; a broadly contemporary phase of flash flooding is noted along the plains around Khania in Western Crete during the later Middle Bronze Age (Moody 2000).

The climate of the Late Bronze Age continued on a trend of increasing seasonality; however the period was climatically one of the most unstable of the Holocene, as precipitation regimes and temperatures fluctuated repeatedly, indicating a gradually decreasing likelihood of stable malarial transmission in favour of epidemic and seasonal transmission. Winter temperatures appear to have decreased further in c. 1550 cal. BC (3500 cal. BP)[68]; foraminifera analysis from LC21 indicates pronounced winter cooling, with SSTs at c. 12 ˚C (figure 3.4) (Stuvier *et al.* 1993; Bond *et al.* 2001; Rohling *et al.* 2002). Temperatures subsequently increased sharply after c. 1550 cal. BC (3500 cal. BP) as summer and winter temperatures increased beyond those of the modern (14-16 ˚C) (Rohling *et al.* 2002). $\delta^{18}O$ data from core LC21 indicate that summer evaporation gradually reduced; a theory which is supported by pollen records from Crete, which indicate that *Tilia,* the drought-intolerant tree, disappeared from all cores during this period (Stuvier *et al.* 1993; Moody *et al.* 1996; Rohling *et al.* 2002; Bottema *et al.* 2003).

[68] 3300±14 ^{14}C yr BP (Reimer *et al.* 2004)

$\delta^{18}O$ data from marine core LC21 from the Aegean basin core indicate a gradual decrease in evaporation levels during the succeeding century; this persisted until 1374-1262 cal. BC (3300-3200 cal. BP)[69], when humidity levels reached those of the modern period and winter SSTs decreased once again to the Holocene minimum (below 12-14 ˚C) (Rohling *et al.* 2002). The brief nadir in winter temperatures is also noted in marine cores from the Adriatic; where data suggests that this event predominantly affected winter and spring temperatures, indicating an increase in seasonality (Sangiorgi *et al.* 2003). This cooling period appears to have been as brief as the previous fluctuation, as winter temperatures increased after approximately one century to between c. 14 ˚C and 16 ˚C (Rohling *et al.* 2002).

Drought conditions appear to have prevailed across the eastern Mediterranean between 1300-1200 cal. BC (3250- 3150 cal. BP)[70], the last century of the Late Bronze Age occupation at Lerna. $\delta^{18}O$ values from marine core LC21 indicate that winter temperatures remained elevated while humidity levels continued to fall; a trend which is mirrored in proxy data from across the eastern Mediterranean (Rohling *et al.* 2002). $\delta^{18}O$ values from speleothems in the Levant indicate a contemporary decline in precipitation that lasted until the end of the Bronze Age and water levels of Lake Van and the Dead Sea decreased abruptly during this period indicating increased aridity (Frumkin 1991; Bar-Matthews *et al.* 1997; Wick *et al.* 2003). Textual evidence from Egypt indicates a further reduction in the Nile flow (Hassan 1997). Anatolian pollen records, although few, indicate a warmer trend, as the vegetation altered in favour of drought-tolerant plants; it should be noted, however, that these plants favour open land and the high frequency may therefore reflect anthropogenic activity rather than climatic change (Eastwood *et al.* 1999).

[69] 3052±16 ^{14}C yr BP - 2972±15 ^{14}C yr BP (Reimer *et al.* 2004)
[70] Commonly dated in marine and pollen cores to 3031±16 ^{14}C yr BP and 2961±16 ^{14}C yr BP (Reimer *et al.* 2004)

Some scholars have suggested that this drought was sufficiently severe to have contributed to the decline of the Mycenaean civilisation (Carpenter 1966; Bryson *et al.* 1974); the theory has since been challenged, however the increasing aridity would undoubtedly have had social and economic effects. Moody (2005a) has suggested that the drought may have prompted a focus on water sources, where cisterns, dams and canal systems were constructed and seemingly defended; a phenomenon which has been noted at many of the larger archaeological sites across southern Greece, such as Athens, Tiryns, Mycenae and the Kopais basin (Dickinson 1994; Moody 2005a).

This extended period of drought coincided with increasingly variable precipitation regimes, as multiple extreme climatic events are reported across the Aegean during this period[71]. Flood deposits have been noted in Attica and at Dhali-Potamia in Cyprus; flash flooding has been reported in alluvial deposits from Frangokastello and Agios Vasilieous on Crete and dramatic flooding deposits, amounting to several metres, have been excavated at Tiryns (Paepe 1980; Zangger 1994; Moody 2000; 2005a; Butzer *et al.* 2005). Scholars have debated whether these events, particularly those linked to the Argive plain, were the result of increased anthropogenic activity; however van Andel (*et al.* 1990) conclude that the event was caused by a combination of both human influences and extreme climatic conditions. These arguments will be considered further in chapter six. The Bronze Age therefore ended within an erratic climatic trend, where temperatures, humidity and rainfall oscillated rapidly and repeatedly.

[71] Each event is dated through archaeological and ceramic evidence to the LHIIIB (Paepe 1980; Zangger 1991; 1994; Moody 2000). The alluvial event at Dhali-Potamia is dated to c. 1900-1100 BC and can only, therefore, be linked to the mid- to Late Bronze Age period (Butzer *et al.* 2007).

The climate and malariogenic capacity of the Bronze Age

Lerna

The site of Lerna, located on the Argive Plain, was occupied throughout the Bronze Age period; the site is suggested to have been settled during Early Helladic II (EHII) and continuously occupied until a final abandonment in the Late Helladic period (LH) (figure 3.2c) (Caskey 1960; 1968). The Bronze Age occupation of Lerna therefore occurred after the termination of the Holocene Humid Period and the introduction of an increasingly arid climate. The Argive Plain, much like the Southern Argolid, is a region of considerable aridity and is therefore suggested to have been particularly vulnerable to the decreasing humidity and repeated drought conditions of the Bronze Age. The modern climatic data for this region is derived from the weather station at Nauplion which was referred to above for the Southern Argolid (figure 3.5); the information will therefore merely be summarised here.

The general climatic trend of the Argive plain is one of hot and arid summers, an aridity which lasts for approximately seven months (April to October), while the winter months are mild and wet, tempered by the proximity to the sea. Rainfall levels vary from 4.3 mm in the height of summer to above 92 mm in mid-winter; frost and, at the higher elevations, snowfall are not uncommon during the winter months and average summer temperatures range between 27.5 ˚C (July/August) and 10 ˚C (January) (Meteorological Office 1915; Darby 1944). Wind systems are suggested to be similar to those of Franchthi Cave, with the coastal positioning of the site indicating particular exposure to south-easterly winds (Theophrastus' *De Ventis*; Poulos *et al.* 1997).

There are few pollen cores from the Argive Plain, the most important deriving from an ancient lake lying 1 km to the north of Lerna (figure 3.3), although the interpretative value of the local cores with regard to regional climatic patterns is severely limited by the increasing

intensity of anthropogenic activities (Jahns 1993). Marine cores C-69 and C-40 are the most local sources of proxy climatic data to the Argive Plain; however both cores represent a wider catchment region and cannot be considered to solely reflect the plain (Geraga *et al.* 2005).

Based on the general climatic trends outlined above, the potential for prolonged transmission seasons and for extended periods of exposure to *P. falciparum* during the Bronze Age period is suggested to have declined as the period progressed (figure 3.9). Annual temperatures largely remained conducive to malarial transmission; with the exception of two brief cooling events, the first during the sixteenth century BC and the second during the fourteenth century BC, temperatures in the southern Aegean remained sufficiently high to support all three vectors, including *Plasmodium falciparum* and certainly would have permitted long, potentially perennial transmission seasons.

The malariogenic capacity of the region would, nonetheless, have been severely limited in comparison with that of the earlier periods of the Holocene due to the termination of the 5000 year long HHP, just prior to the transition to the Bronze Age period. The effects of this event would have been considerable, causing a great decline in humidity and a shift towards a more seasonal precipitation regime, where rainfall predominantly fell during the winter months. The beginning of the Bronze Age and the end of the humid phase can therefore be seen as a definite turning point in the malariogenic capacity of the Aegean, causing irrevocable changes to the projected transmission seasons of the Aegean. Correlations with modern malarial studies would suggest that the abrupt decrease in humidity levels would have reduced mosquito populations, shortening the life-span of the mosquitoes and, in conjunction with higher temperatures, may potentially have desiccated both *Anopheline* eggs and adult vectors. The seasonal distribution of rainfall would furthermore limit water availability, reducing the volume of breeding grounds during the breeding seasons.

The repeated fluctuations of the Bronze Age climate, although on a reasonably large chronological scale, are suggested to have resulted in an increasingly variable malariogenic capacity. The oscillating temperatures and humidity levels, which both peaked to the highest and declined to the lowest levels of the Holocene during this period, are suggested to have been extremely disruptive to any existing disease patterns, as the potential for reproduction, survival rate, population density and biting habits of the vectors would have altered with the variable climatic conditions. The repeated droughts of the Bronze Age are suggested to have reduced the malariogenic capacity and imposed limitations on potential transmission patterns; the most pronounced of these being the global drought of c. 2200-1900/1800 BC (c. 4150-3950 cal. BP)[72]. This climatic event is suggested to have sharply curtailed the malariogenic capacity of southern Greece; the abrupt decline in humidity levels, high temperatures and decreased water levels recorded in global proxy data, would indicate fast development time, but low *Anopheline* survival rates.

While the extended nature of this drought would have theoretically diminished vector populations, it may be argued that the coastal positioning of Lerna would indicate higher humidity levels despite the prevailing drought conditions (Darby 1944). This would permit increased longevity for the vectors. Under such circumstances, the reduction in water availability could therefore be seen to favour the more drought-tolerant vectors such as *A. sacharovi* and *A. superpictus.* The lower precipitation levels would result in reduced river flow, dried lakes, river beds, ditches and potential expansion of marshland, producing a high volume of standing surface water and thereby promoting increased population densities of drought-tolerant vectors. Assuming a higher humidity level for coastal environments, a high

[72] 3777±13 ^{14}C yr BP – 3622±14 ^{14}C yr BP (Reimer *et al.* 2004)

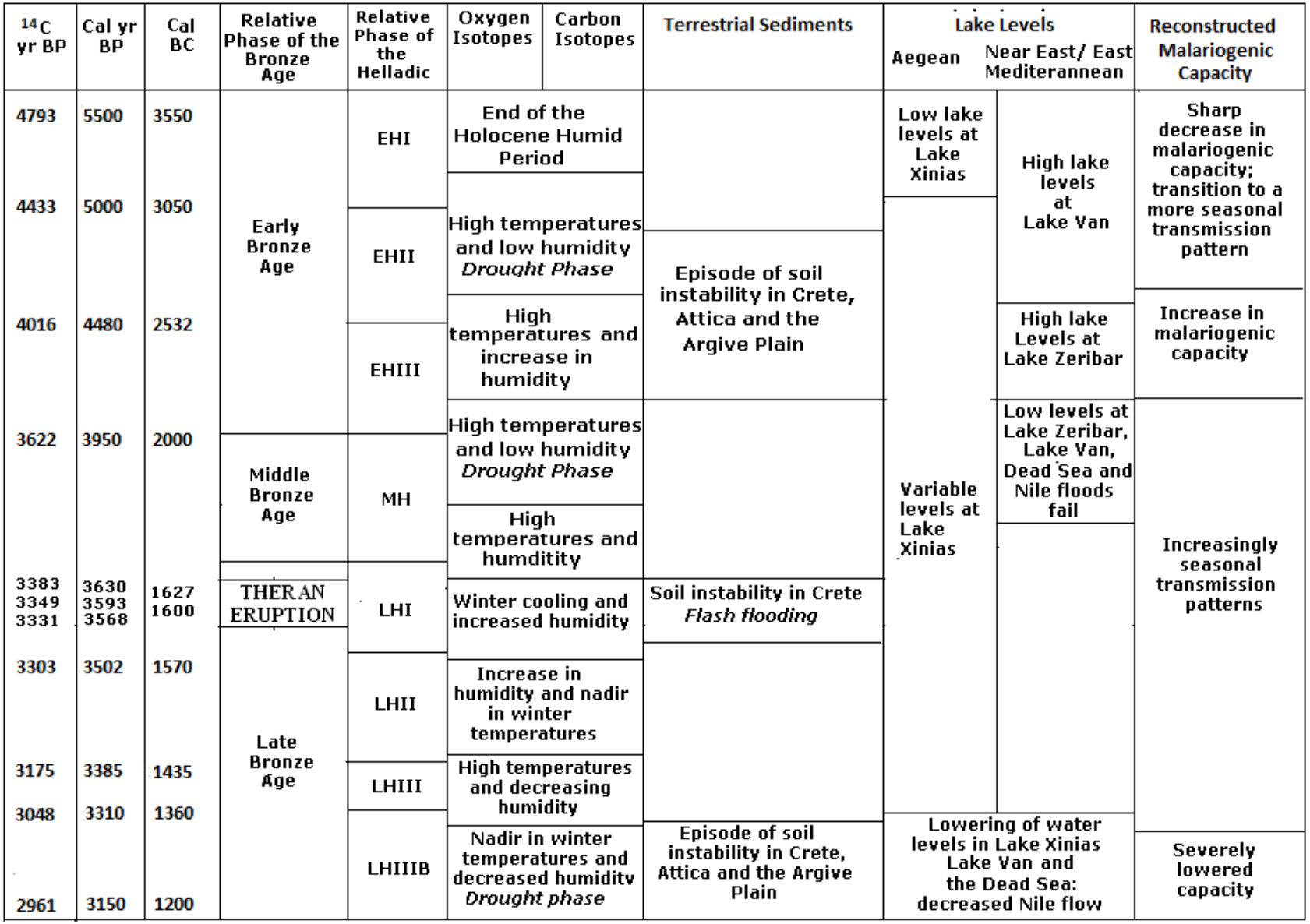


Fig. 3.9. Climatic trends and projected malariogenic capacity of the Aegean: 3530- 1200 cal. BC (5500-3200 cal. BP)

malariogenic capacity within particular environmental foci can be proposed. Such circumstances would potentially result in a greater incidence of malaria; transmission intensity can increase under such climatic conditions and can result in virulent epidemic-endemic cycles (Macdonald 1957; Bruce-Chwatt 1980). The effects of these drought periods on the environment of the Argive plain will be considered in chapter six.

It is proposed that the climatic events following the eruption of Thera in c. 1627-1600 cal. BC (3687-3580 cal. BP)[73] (Freidrich *et al.* 2006) would have again reduced the potential for perennial transmission; while the higher levels of humidity would have permitted a longer lifespan for the adult *Anopheles* and increased the survival rate of mosquito eggs and larvae, the gradually decreasing winter temperatures would shorten the transmission seasons (Bruce-Chwatt 1980). The fluctuations in precipitation noted in some proxy data sources would have contributed to a seasonal form of transmission, potentially encouraging epidemic transmission in regions which were most affected. The high temperatures of the subsequent centuries may have increased this capacity; however the steadily declining humidity levels throughout these periods would indicate that the malariogenic capacity would have been limited in comparison with that of the previous phases of prehistory.

The increasing aridity and fluctuating temperatures of the fifteenth and fourteenth century BC culminated in the drought of LHIIIB (c. 1300-1200 BC) (figure 3.9), which is suggested to have produced the lowest malariogenic capacity of the chronological periods considered in this thesis. The combination of low (although increasing) winter, and possibly spring, temperatures and low humidity levels (Rohling *et al.* 2002; Sangiorgi *et al.* 2003), would result in shortened transmission seasons, slower reproduction and sporogonic cycles, shorter *Anopheline* life spans and a lower survival rate for *Anopheline* eggs and larvae (Macdonald

[73] The mean date from four dates of 3383±11, 3372±12; 3349±12 and 3331±10 ^{14}C yr BP (Freidrich *et al.* 2006).

1957; Clements 1963). This declining trend was, however, punctuated by extreme climatic events such as, for example, the flooding episodes noted in archaeological records along the Argive Plain during EHII and again in LHIIIB. Such events, resulting in the expansion of breeding grounds, commonly result in a higher malariogenic capacity and even if the episode is brief, infection rates would be expected to increase. Modern studies would indicate that the combination of climatic events during both EHII and LHIIIB would create potential for highly unstable disease patterns; the high temperatures and aridity, punctuated by brief episodes of excess rainfall or increased humidity are key factors in triggering explosive regional epidemics (Bouma *et al.* 1994a,b; Lindsay *et al.* 1996a,b; Leishout *et al.* 2004; Pascual *et al.* 2006). The climatic conditions of both EHII and LHIIIB are therefore suggested to have potentially resulted in epidemic or unstable transmission.

The palaeoclimatic data would therefore once again support Angel's (1971) interpretation of a declining capacity for endemic malaria throughout the Bronze Age. The climatic data indicates a steadily decreasing malariogenic capacity, as the lower humidity levels following the termination of the HHP and increasing seasonality are suggested to have been less suitable for endemic or stable transmission of malaria. Exposure to malarial vectors would be reduced under such conditions, supporting the contention that the prevalence of a genetic immunity could have decreased in frequency. However, contrary to Angel's (1971) theory, it is suggested that the increasingly erratic climatic patterns of the Middle to Late Bronze Age would have produced a fluctuating malariogenic capacity; based on modern studies, transmission is therefore tentatively suggested to have become more intense, producing a seasonal or epidemic pattern.

Discussion

Osteological evidence led Angel (1966; 1969a; 1971; 1973) to hypothesise that β-thalassemia, and *P. falciparum* had been introduced into, and established within, the Aegean by the Lower Mesolithic (8700-8000 BC) (figure 3.2a) and had increased in frequency into the Neolithic (7000- 3300 BC) before sharply declining through the Bronze Age (3300-1200 BC) (Angel 1971; 1972). A reconstruction of the general palaeoclimatic trends of the Aegean would largely support the contention of a high malariogenic capacity. The overall climatic pattern of the Aegean would, when referring to modern malarial studies, indicate a model which would broadly match that suggested by Angel (1969a; 1971, 1972).

The climate of the Aegean is suggested to have become highly conducive to all three forms of malarial parasite and the tropical *Anopheline* vectors following the transition to the Holocene. The combination of the high humidity levels, elevated annual temperatures, annual distribution of rainfall and increased water availability would appear ideal for transmission and would certainly, in theory, support the development cycles of *P. falciparum* and sustain the tropical vectors of that strain. It is therefore suggested that the climatic improvements of the Lower Mesolithic period may have facilitated the geographical expansion of both the parasite and the 'tropical' vectors, *A. superpictus* and *A. sacharovi* from Africa and the Near East, and have plausibly supported both within the Aegean after the climatic amelioration of c. 9050-8550 cal. BC (c. 11000-10500 cal. BP)[74].

The suggested endemicity of the disease and the suggested increase in frequency of the genetic condition during the succeeding centuries of the Mesolithic and, particularly during the Neolithic, is again climatically plausible. The malariogenic capacity of the Early

[74] 9560±21 ^{14}C yr BP – 9283±17 ^{14}C yr BP (Reimer *et al.* 2004)

Holocene reached a zenith when the Holocene Humid Period began in c. 7050 BC (c. 9000 cal. BP)[75]; a well-documented period of excessively high humidity levels, coinciding with elevated annual temperatures and annual precipitation regimes. The transition resulted in a 'fundamental drop in … [climatic]… variability' (Borroughs 2005: 55); the clear reduction in seasonal variance in both rainfall and temperature and the increase in water availability, noted in both the northern and southern regions of the mainland, would indicate that climatic conditions were far more conducive to malaria transmission than those of the Aegean in recent history. Correlations with modern malaria studies indicate that such conditions would undoubtedly support a higher abundance of vectors and would easily facilitate perennial transmission of all three *Plasmodiae*, including the virulent *P. falciparum.* From a climatic perspective, the conditions of the early Holocene appear ideal for *P. falciparum* and the tropical vectors to have become securely established and successful within the Aegean.

A particularly important factor of this phase with regards to malarial transmission was perhaps the stability of the new climatic regime; this period of exceptional warmth and humidity persisted and even increased between the beginning of the Holocene and the abrupt and dramatic deterioration of winter temperatures at c. 6250 cal. BC (8200 cal. BP)[76]. Conditions during this period appear extremely viable for the success of the *P. falciparum* parasite and the *Anopheles* vectors and would suggest a strong and increasing potential for endemic transmission between the Lower Mesolithic and Early Neolithic which would support Angel's (1971; 1972) theory for a high malariogenic capacity during this period.

The pronounced winter cooling and aridity during the Early Neolithic at c. 6250 cal. BC (8200 cal. BP) and again at 5150 cal. BC (7100 cal. BP)[77] would have severely altered the

[75] 8056 ± 13 ^{14}C yr BP (Reimer *et al.* 2004)
[76] 7415 ± 18 ^{14}C yr BP (Reimer *et al.* 2004)
[77] 7415±18 ^{14}C yr BP and 4555± 14 ^{14}C yr BP (Reimer *et al.* 2004)

malariogenic capacity of the Aegean, limiting potential transmission seasons throughout the duration of the climatic events. While it is suggested that the former event would have limited transmission patterns, it is noted that the humidity levels remained higher than those of the modern; combined with the continuing warm temperatures, it is suggested that these conditions would have continued to support the parasites and *Anopheline* vectors, albeit on a more seasonal transmission regime. The latter event, however, marks the termination of the HHP in the northern regions of Greece; an event which appears to have been delayed until 4450 cal. BC (6400 cal. BP) to 3350 cal. BC (5300 cal. BP)[78] in the southern regions; this climatic deterioration is suggested to have been the 'turning point' in the malariogenic capacity of the Aegean. The lower humidity levels and increasingly seasonal precipitation regimes would have limited transmission seasons and resulted in the gradual reduction in the length of the malarial season.

This more arid climatic trend would have increased as the Bronze Age progressed and as seasonal variability became more enhanced. The climatic fluctuations in humidity, rainfall and temperatures, combined with episodes of severe and prolonged drought which persisted within this trend, would have resulted in an increasingly irregular malariogenic capacity, promoting sharp increases in vector populations and in infection rates. Exposure to the malarial vector would therefore have become erratic and stable malaria transmission is suggested to have become increasingly rare.

The palaeoclimatic data for the prehistory of the Aegean would therefore indicate that the conditions between the Upper Mesolithic and Late Bronze Age were suitable for both the *Anopheles* vectors and the malarial parasites, including *P. falciparum,* to have become established within the Aegean and to have thrived. The general climatic trend of increasing

[78] 5892±17 ^{14}C yr BP/ 4793±13 ^{14}C yr BP (Reimer *et al.* 2004; Gougou *et al.* 2007)

seasonality indicates a transmission pattern that correlates well with Angel's (1966; 1969a; 1971; 1973) skeletal evidence; the highest frequencies of genetic immunity occur during a period which climatically appears to have been extremely favourable for endemic malaria, while the declining frequency of β-thalassemia coincides with a progressively seasonal and unstable climate, which would be expected to result in less consistent but more intense exposure to the disease.

It must also be reiterated that the projected malariogenic capacity outlined within this chapter is based entirely on the general climatic trends; the rarity of site- specific or high resolution climatic data limits the accuracy and scope of the reconstruction. The aim of this chapter is specifically to investigate the overall climatic trends of the Aegean in order to ascertain whether the parasite and vectors could have been supported in a similar pattern as suggested by Angel's (1971) studies; in this regard, the palaeoclimatic reconstruction has been successful. It is not suggested that the climatic trends were entirely responsible for the changing frequencies of the suggested genetic immunity; there are many other factors which would have determined the malariogenic capacity. Environmental conditions, population dynamics, social and economic systems, and population migrations would each play a crucial role in malaria patterns. These factors will be considered with regards to the climatic data on a site specific basis in the following chapters. It is concluded here, however, that reconstructions of the general climatic trends of the Aegean during the Mesolithic to Late Bronze Age would support the theory of a high, although gradually decreasing, malariogenic capacity during the prehistory of the Aegean.

Chapter Four:

Palaeoenvironmental Reconstructions: Malaria and the Mesolithic to Middle Neolithic of Franchthi Cave, Southern Argolid

Franchthi Cave, lying on the western coast of the Southern Argolid, is one of very few Mesolithic settlements on the Greek mainland. Reconstructions of the malariogenic capacity of this site are of particular interest to this thesis, as the occupation of the site encompasses the transition from hunter-gatherer to early agricultural life; a crucial change in anthropogenic behaviour that would have altered the malariogenic capacity significantly. Archaeological excavations have revealed a wealth of information, affording an extraordinary glimpse into life, diet and health. The occupation of the site is suggested to have covered approximately 25,000 years; the chronology of the Mesolithic to Middle Neolithic occupation, periods for which osteological data is available, is outlined in figure 4.1.

Modern malarial studies

Before a reconstruction of the Mesolithic landscape and malariogenic capacity is attempted, recent malarial studies from the Argive Plain will be briefly considered as these may provide a frame of reference for the potential malariogenic capacity of the region during prehistory. There is a dearth of studies concerning malaria in the Southern Argolid during modern history; however detailed studies into malarial transmission patterns were undertaken between 1909 and 1940 across the Peloponnese (Lividas *et al.* 1941) and between 1930 and 1933 on the northern Argive Plain (Balfour 1935; 1936). Due to the relative proximity of this region to the Southern Argolid, these studies will be used as a general guide to the vectors, seasonal distribution and malariogenic capacity of southern Greece in more recent history. Studies indicate that the highly variable temperatures and rainfall levels of the region, noted in chapter three, would have been partly responsible for the highly erratic malarial patterns

reported in the area; reproduction, development and biting behaviour of the *Anopheline* vectors oscillated along with these weather patterns, resulting in a highly variable intensity of infection (Balfour 1935; Lividas *et al.* 1941; Martin *et al.* 1995; Lindsay *et al.* 1996; Zhou *et al.* 2004). Balfour's (1935; 1936) study of malaria patterns between 1930 and 1933 shows that an endemic-epidemic cycle predominated in the region, with moderate to severe endemicity and severe epidemics correlating closely with rainfall patterns. Supported by a review of malaria frequencies in Greece (Lividas *et al.* 1941), Balfour's (1935) data indicated that years of evenly distributed rainfall led to moderate to severe endemicity, while erratic rainfall resulted in fluctuating disease patterns. Wet winters followed by wet springs would frequently result in malaria epidemics, producing high mosquito population densities and high frequencies of *P. falciparum*; a dry winter and spring would cause an increase in vectors that favour temporary breeding grounds, such as *A. superpictus*, again resulting in epidemic conditions.

Balfours' (1935) study found *A. sacharovi* to be the primary vector of villages located in proximity to coastal waters and marshland, with *A. superpictus* and *A. maculipennis* in high densities. *A. superpictus* was the primary vector in villages situated further inland close to foothills, favouring river beds surrounded by overhanging vegetation for oviposition; *A. sacharovi* and *A. maculipennis* appeared in lesser volumes but both sub-species contributed significantly to the malarial burden. Secondary vectors, as listed in chapter one (figure 1.6), were prevalent although *A. plumbeus* was not reported in this region during the twentieth century; this may be explained by the extensive deforestation of the Argive Plain during the last two centuries which removed the vectors habitat. Records show that during an average year of moderate to severe endemicity, these vector populations increased in April, peaking in June and again in early August. Autumn increases in malarial infection rates were primarily linked to *A. superpictus* populations; these continued into October, and decreased

during December; the remaining four months of the year saw low rates of infection rate (Balfour 1935; Lividas *et al.* 1941; 1948). Balfour (1935) noted elevated infection rates in this region, with high numbers of mixed infections.

The vector populations of modern history cannot, of course, be projected directly into the past; the distribution of the *Anopheline* vectors during the 1900's was undoubtedly enhanced by expansive anthropogenic activities that could not have been implemented by prehistoric societies. Agriculture, livestock grazing, extensive land clearance, alterations to hydrological systems and population mobility of the early twentieth century increased the viability of the local environment for the primary *Anopheline* vectors (Lividas *et al.* 1941). These studies do, however, serve to briefly illustrate the relationship between the topographical relief, human activities and the main malarial vectors of the region.

Chronological Phase	Lab Sample	^{14}C Age	Cal. BP 2σ	Cal. BC 2σ	Median cal. BC	Chronological period cal. BC (Perlès 2001)	Reference
Lower Mesolithic	P-2227 P-2103 P-2102 P-2108 P-2228 P-1518 P-1517	9430±160 9300±100 9290±100 9250±120 9060±110 8940±100 9030±110	11166-10290 10735-10243 10721-10241 10740-10199 10554-9833 10250-9698 10494-9779	9217-8341 8786-8294 8772-8282 8791-8250 8605-7884 8301-7749 8545-7830	8762 8543 8530 8493 8272 8079 8225	8700- 8000	(1,3,4)
Upper Mesolithic	P-1666 P-2096 P-2107	8740±110 8710±100 8530±90	10155-9538 10150-9529 9732-9303	8206-7589 8201-7580 7783-7354	7832 7781 7569	8000-7000	(1,3,4)
Final Mesolithic	P-1536 P-1526	8190±80 8020±80	9408-8996 9123-8631	7459-7047 7174-6682	7214 7053		
Initial (Aceramic) Neolithic	P-2095 P-2094 P-1527 P-1392	7980±110 7930±100 7900±90 7790±140	9189-8544 9029-8521 9007-8541 9002-8372	7240-6595 7080-6572 7058-6592 7053-6423	6889 6838 6803 6674	7000-6450	(1,3,4)
Early Neolithic	P-1525 P-1667 P-1399	7700±80 7280±90 7190±110	8636-8371 8315-7950 8302-7788	6687-6422 6366-6001 6353-5839	6540 6152 6069	6450-5900	(1,3,4)
Middle Neolithic	P-2093 Beta-15613 P-2235 P-1662 P-1824 P-1537 Beta-15614 Beta-15612	6940±90 6860±120 6750±80 6690±90 6670±70 6650±80 6720±100 6600±250	7942-7617 7941-7509 7749-7464 7671-7435 7656-7434 7658-7427 7757-7428 7958-6960	5993-5668 5992-5560 5800-5515 5720-5480 5707-5485 5709-5478 5808-5479 6009-5011	5829 5765 5660 5610 5591 5580 5637 5536	5900-5300	(1,2,3,4,5)

Fig. 4.1. Chronology of Franchthi Cave from Mesolithic-Middle Neolithic occupation. Calibrated by author using OxCal 4.1. (**1**) Jacobsen *et al.* 1987 **(2)** Gifford 1990 **(3)** Perlés 2001; (**4**) Reingruber *et al*. 2005; **(5)** Vitelli *et al.* 1999.

Reconstruction of the environment and malariogenic capacity of Franchthi Cave

The Mesolithic (8700-7000 cal. BC/ 10650-8950 cal. BP)

The environment and topography surrounding Franchthi Cave during the Mesolithic was, theoretically, certainly sufficiently varied for a wide range of vector species to have co-existed and thrived. The cave, situated on the western coast of the Southern Argolid, lay within an extremely diverse landscape, encompassing coastal plain, hills, valleys and expansive mountain ranges (figure 4.2). The Dhidhima mountain range circles the cave to the north, reaching up to 1113 m, and more moderate elevations of 400 m lie to the south of the site (Hansen 1991). The topography of the region is predominantly of low, rolling hills, separated by broad intramontane valleys, such as the Fourni valley to the north-east of the cave, and the Kiladha basin to the south-west of the cave. These valleys channel two rivers and numerous streams and springs towards the coast, some in extremely close proximity to the cave. The modern day Fourni River is ephemeral and often dry during the summer months, while the Kiladha River, lying in close proximity to Franchthi Cave (hereafter termed Franchthi River), is now dry all year round (figure 4.4) (van Andel 1980).

A reconstruction of the coastal evolution of the region suggests that considerable ecological changes occurred during the occupation of the cave. The increasing global temperatures of the early Holocene caused large quantities of water to be released from continental ice caps, resulting in eustatic sea-level changes (van Andel *et al.* 1980; *et al.* 1982). Franchthi Cave now directly overlooks the coastline (figure 4.3); however during the Last Glacial Maximum the occupants of the cave are suggested to have overlooked a vast coastal plain, where the shoreline lay up to 7 km away (figure 4.4) (Van Andel *et al.* 1982).

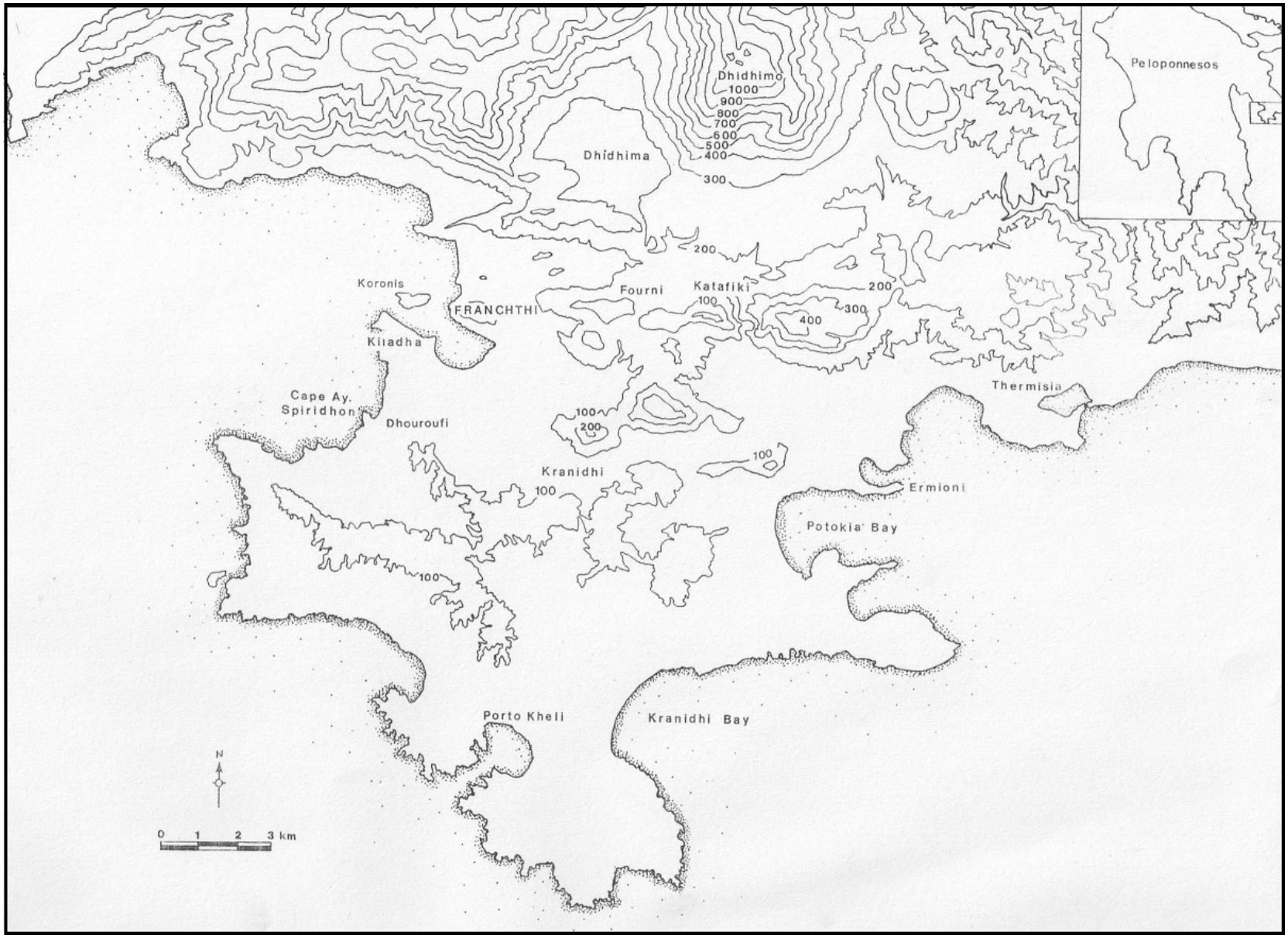


Fig. 4.2. Topography of the Southern Argolid (*After* Hansen 1991: fig. 1: pg. 2).

Fig. 4.3. The modern positioning of Franchthi Cave (*After* Gkioni 2004: fig 2: pg. 122).

The sea gradually transgressed this plain, a process which had slowed by the beginning of the Mesolithic period, leaving the coast approximately 2 km from the mouth of the cave. The coastal lowlands, previously an expansive and valuable area of grazing land for large game, were severely reduced to approximately one fifth of the Palaeolithic coastal plain (Shackleton *et al.* 1986). The Franchthi headland therefore underwent a significant environment change which resulted in a diminished coastal plain of approximately 17 km² (van Andel *et al.* 1980; *et al.* 1987; Wilkinson *et al.* 1990). Molluscan studies at Franchthi Cave indicate that the coastal zone altered considerably due to this transgression (figure 4.4). The abundance of *Patella* spp. (Common Limpet), *Mondonata* spp. (sea snail) and *Gibbula* spp. (sea snail) within the Mesolithic molluscan assemblage indicates that the marshland and lagoons that predominated during the Palaeolithic were replaced with an exclusively rocky coastline, with some areas of cobble and shingle (Shackleton *et al.* 1986). The total decline in marshland is suggested to have limited the volume of potential vector breeding grounds, thereby resulting in a lower malariogenic capacity; the prevalence of rock pools, as indicated by the molluscan remains, would, however, serve as breeding grounds for the saline tolerant vectors (Muirhead-Thomson 1951; Bruce-Chwatt *et al.* 1980).

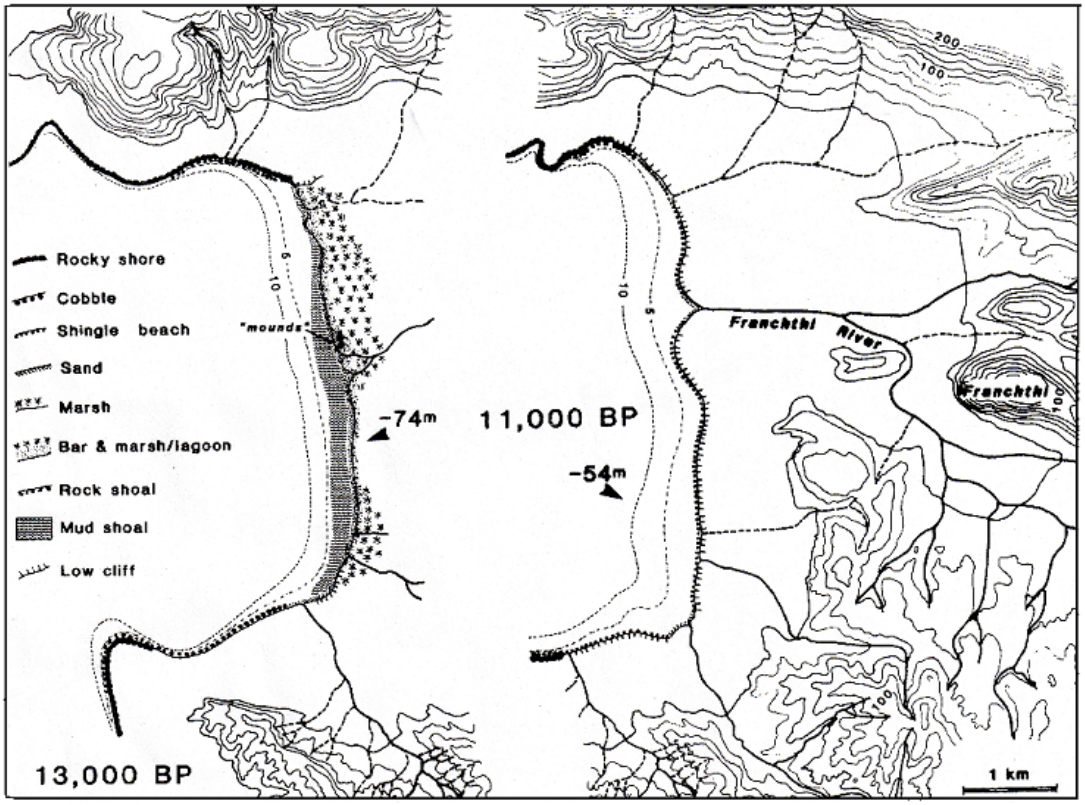


Fig. 4.4: The Palaeolithic and Mesolithic shoreline at Franchthi Cave (*After* Shackleton *et al.* 1986: fig. 9: pg. 137).

These pools would have provided especially viable environments if in proximity to the fresh water influxes from the Franchthi River (discussed further below) and may therefore have created breeding grounds for the *Anopheline* vectors that tolerate mild salinity. *A. sacharovi,* is the most tolerant of such conditions, while *A. superpictus, A. atroparvus, A. algeriensis* may also have bred in such waters (Lividas *et al.* 1941; Bruce-Chwatt 1980; Yaghoobi-Ershadi *et al.* 2001). These potential breeding grounds, lying within the flight range of the *Anopheline* vectors, would have represented some threat to the occupants of the cave, although the malariogenic capacity of this rocky shore would undoubtedly have been minimal.

The prevalence of fresh water in the region would have augmented this capacity. Sedimentological analysis indicates two river basins flanked the cave; one to the north in the

Fourni valley and to the south in the Kiladha basin. These rivers merged to form the Franchthi River to the west of the cave (figure 4.4). Seismic profiling of the river bed indicate that these rivers were permanent during the Mesolithic, producing a sustained and elevated flow until c. 5050 to 4050 BC (c. 7000 to 6000 BP)[79], when the flow became more ephemeral (van Andel *et al.* 1980).

Karstic springs are also prolific in the area due to the limestone bedrock of the region. Sinkholes, or 'katavothroi', created by gradual erosive action, absorb rainfall and snow-melt directly and where the subterranean channels become blocked or reach the underlying, impermeable flysch[80] surface, the water is forced to the surface and forms a spring, often at some distance from the point of absorption. The cave itself is a karstic feature and is surrounded by at least four known sinkholes; two lie within the Franchthi headland, to the east and southeast of the cave. A larger karstic basin lies at c. 5 km, close to the modern town of Dhidhima (figure 4.2) and a further sinkhole occurs near Iliokastro at c. 13 km east to north east of the cave. These systems may be linked to Franchthi Cave, channelling the rainfall and snow melt from the uplands to the coast; however the connection between these systems is unverified (Farrand 2000). That the cave is part of an extensive karstic network is certain, as excavations from Franchthi identified a large pool of water of varying levels of salinity at the rear of the cave, suggesting a connection to both fresh water systems and to the salt waters of Kiladha Bay (Jacobsen 1969; Farrand 2000).

The water from these systems is suggested to have been channelled towards the coast and the Franchthi headland; geomorphological studies indicate that numerous springs emerged along the valleys, margins of lowland basins, and particularly along the coastal zone during the

[79] These are inferred ages based on sedimentological studies (van Andel *et al.* 1980)
[80] A sequence of sedimentary rocks formed in deep sea environments at convergent plates during stages of continental collision; predominantly composed of sandstone, siltstone and clay (Higgins *et al.* 1996)

early Holocene (figure 4.5) (van Andel *et al.* 1980). Many of these are now inactive as the subterranean reservoirs have been tapped by wells, contributing to the arid conditions of the region; the presence of perennial streams in the eastern valleys where very few wells have been sunk, has led Jameson (*et al.* 1994) to suggest that "the current scarcity of water [in the Southern Argolid] is not representative of the past" (1994: 170). Geophysical surveys of the coastline confirm this, identifying multiple springs that are now submerged due to sea level rises, which were active to the east and the north of the cave during the Mesolithic and Neolithic occupation of the cave (van Andel *et al.* 1983; Jameson *et al.* 1994). Evidence for elevated precipitation rates during these periods, noted in chapter three, would suggest that the volume of water produced by these systems was high (van Andel *et al.* 1980; Farrand *et al.* 2000).

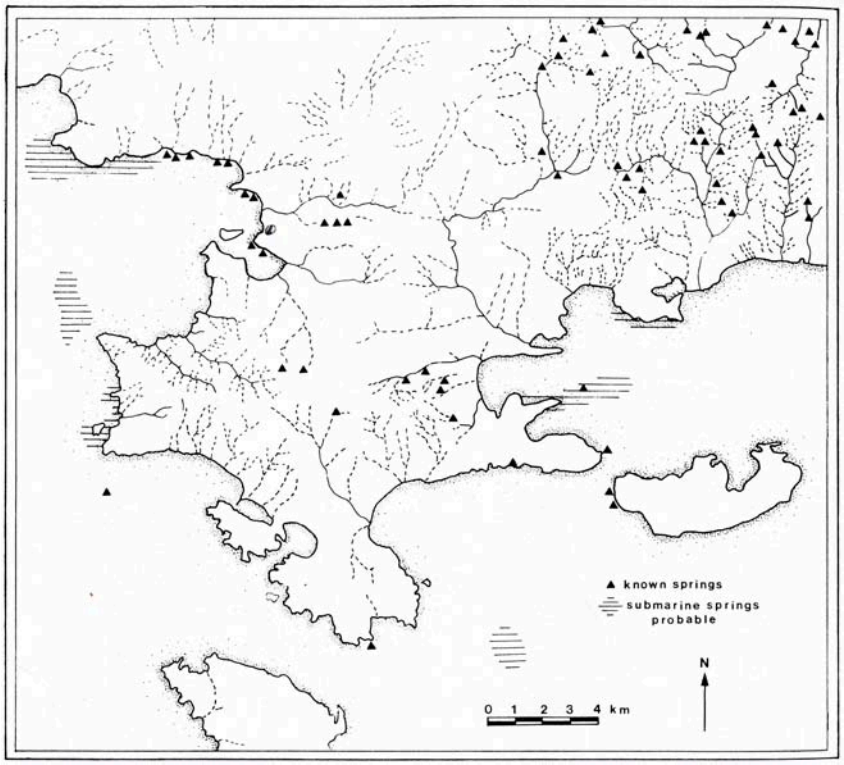


Fig. 4.5. Springs and rivers in the Southern Argolid. The springs along the coastline and the rivers to the east and to the north of Franchthi cave are considered to have been active during the Mesolithic and Neolithic period (*After* van Andel *et al.* 1987; fig. 5: pg. 19).

The volume of water, both fresh and brackish, in the area therefore appears to have been considerable and presumably the reason that the site was so attractive to prehistoric populations. Such convenience would however have come at a cost, as these significant quantities of water could have led to a high malariogenic capacity within mere metres of the mouth of the cave and even within the interior of the cave. Vector populations in the immediate locality could potentially have been high, as many *Anopheline* species would favour these water sources for oviposition; whether viable as breeding grounds or not, it is suggested that the risk of infection in the locality would have been high, as adult females will bite when seeking to oviposit (Le Menach *et al.* 2005). The dark, cool and damp environment of the interior may further have increased the risk of infection, attracting the mosquitoes into the human dwelling when they sought shelter during the heat of the day. The cave would not have offered much protection against vectors, being open to elements and lined with innumerable fissures and cracks with the rock. Vectors could easily access the interior and the occupants within.

The vegetative cover of the landscape surrounding Franchthi Cave is significant to the potential distribution of the *Anopheline* vectors; it is, however, difficult to reconstruct as there are no local terrestrial pollen cores that date to this period. Previous studies into the environment of the Mesolithic (Bottema 1990; Hansen 1991) have therefore referred to cores from northern Greece. These cores, such as Ioannina, Tenaghi Philippon, Gramousi and Rezina, would indicate an increase in deciduous pollen, such as *Quercus, Tilia, Ulmus, Fraxinus* and *Ilex* (L.) (holly), as the postglacial conditions of the Younger Dryas receded (Bottema 1974; Turner *et al.* 1975; Willis 1993a,b,c). Hansen (1991) suggested similar taxa for the Southern Argolid. This is confirmed by pollen records from marine core C-40, sited in the Myrtoon basin in the southern Aegean Sea; suggested to have a local rather than regional catchment area, the pollen data indicates that *Pistacia* and deciduous pollen, such as *Ostrya*,

Ulmus, *Fraxinus* and *Tilia* become relatively abundant as the HHP began (this is dated with reference to the deposition of sapropel 1 in C-40 and C-69 in c. 7550/7050 cal. BC (c. 9500/9000 cal. BP)[81] (Geraga *et al.* 2000; 2005).

Hansen (1991) suggests that the lower precipitation rates of the Southern Argolid in comparison with northern Greece would have resulted in an open, parkland landscape during the Mesolithic, rather than the rich oak forest reconstructed from northern pollen cores (Bottema 1974). The presence of *Pistacia atlantica* (Desf.) (pistachio), *Prunus dulcis* (Mill.) (almond) and *Vitis* spp. (wild grape) within the macrobotanical remains dating to the Lower and Upper Mesolithic occupational layers from Franchthi Cave would support this theory, as these species are sun-loving and cannot live in heavy or dense woodland, preferring direct sunlight and an open landscape (Hansen *et al.* 1978; Hansen 1991). The macrobotanical remains from Franchthi Cave would furthermore support the contention that the climate had become milder as *Pistachia* and *Prunus* are both intolerant of frost, rather favouring mild winters and moderate winter to spring rainfall. The presence of *Vitis* in the floral assemblage from the Upper Mesolithic would indicate both milder winters and warmer summer temperatures, as the plant is intolerant to frost and requires a long growing season with minimum temperatures of 18°C in order that fruit may be produced (Hansen 1991; Duke *et al.* 1993). This would again suggest viable conditions for the successful completion of both vector and *Plasmodiae.*

Based on the available macrobotanical and pollen data, van Andel (*et al.* 1987) and Hansen (1991) propose that *Quercus*, *Tilia*, *Ostrya* and *Fraxinus* grew along the valley floors and better watered upland plateaus, as suggested for the northern Greek cores, while the steep limestone slopes surrounding the site were more likely to be covered with maquis or other

[81] 8492±17 ^{14}C yr BP -8056±13 ^{14}C yr BP (Reimer *et al.* 2004).

low to intermediate shrub communities (Bottema 1974; Turner *et al.* 1975; Willis 1993a,b). This latter suggestion is based on the presumption that the thin top soil and the level of exposure generally found in these environments would preclude woodland growth (van Andel *et al.* 1987; Hansen 1991). These areas, and perhaps the coastal plain, are suggested to be covered with shrub communities which favour rocky slopes and open ground, such as *Pistacia, Pyrus amygdaliformis* (Vill.) (wild pear) and *Celtis* (L.) (hackberry), species that were well represented in the floral assemblage from Franchthi Cave (van Andel *et al.* 1987; Hansen 1991; Jameson *et al.* 1994).

Evidence for the vegetation cover of the landscape is also found in the faunal assemblage from the Mesolithic occupation layers; a reconstruction of which appears to support the interpretation of the pollen records (Payne 1975). The abundance of smaller mammals and birds reflects an increasing volume of open woodland (Jacobsen 1973; Payne 1975), while Payne (1975) suggests that the decreased frequencies of *Bos* (L., 1758) (wild cattle) and high frequencies of *Capreolus capreolus* (L., 1758) (roe deer), *Meles meles* (L., 1762) (badger) and *Felis silvestris* (Schreber., 1775) (wild cat) within the Mesolithic assemblage are indicative of woodland cover. The presence of woodland fringe species, such as *Lepus* (L., 1758) (hare) reflect areas of open grassland; this is supported by the interpretation of the rodent assemblage. Two vole species were identified: *Microtus* (Schrank, 1798) which indicates open grassland and *Pitymys* (Mcmurtrie, 1831), which suggests areas of grass and scrubland (Payne 1975; 1982; 1985). The low mobility of the latter species indicates that these open environments lay in the immediate environs of the cave (Payne 1985).

The faunal and archaeobotanical data would therefore permit a reconstruction of the local vegetation during the Upper and Lower Mesolithic. Grassland meadows mixed with trees and shrubs are suggested to have covered the wetter and flatter areas surrounding the cave and

along the coastal plain, while the limestone hills would have been covered with maquis and the valleys to the north-east of the cave would have supported scrubland and open woodland (Payne 1975; 1982; 1985). This landscape mosaic would be extremely suitable for a wide range of the Mediterranean *Anopheline* vectors; dense woodland is not generally favourable to most vectors known to thrive in the Aegean region, however *A. plumbeus* may have been particularly prolific amongst the wooded zones (Blacklock *et al.* 1920b). The fringes of the wooded areas would have provided viable habitats for *A. maculipennis,* which will oviposit within shaded water (Hackett 1937). The scrub and grass land of the coastal plain, valleys and limestone slopes, would provide highly viable habitats for *A. maculipennis, A. superpictus* and *A. sacharovi,* particularly due to the intersection of the former two environments by both rivers and karstic streams (Becker 2003).

The significant environmental changes brought about by the climatic amelioration would therefore lend credence to the hypothesis of a high malariogenic capacity in the proximity of Franchthi Cave during the early Mesolithic. The increase in open woodland, combined with the high volume of both fresh and brackish water in close proximity to the cave, would potentially support a variety of *Anopheline* vectors. The mosaic of habitats is suggested to have been particularly disadvantageous to the Early Mesolithic populations, as coexistence of these various vectors would permit an overlap of their behavioural traits, exposing the occupants to different types of biting behaviour (i.e. endophagic and exophagic vectors), extend biting times and, most significantly, extend the transmission seasons.

The vulnerability of the occupants to malaria infection would have largely been determined by settlement patterns and economic behaviour of the Mesolithic inhabitants. The first issue to address is the population sizes and occupation patterns of Franchthi Cave. Perlès (2003) suggests that the populations of both the Upper and Lower Mesolithic periods were small, as

the diet, largely composed of food stuffs with a high energetic cost, would be insufficient to sustain a larger population. The occupation patterns of the cave have long been debated; based on the floral assemblages and the high density of flot per 100 years, Hansen (1991) suggests sedentary or semi-sedentary occupation. This is supported by sedimentological studies within the cave which indicate a deposition rate of 250 cm per 100 years during the Lower Mesolithic, compared to only 4–7 cm per 100 years during the Upper Palaeolithic, indicating intensive use of the cave during the Mesolithic period (Farrand 1993; 2000). Floral remains would indicate that the occupants were active in the area between spring and autumn, while oxygen isotope analysis of molluscan remains indicates that certain species were foraged during all four seasons, suggesting that the cave was inhabited the year round (Deith *et al.* 1988).

Perlès (2003) cautions that this evidence may indicate no more than repeated seasonal use of the cave, rather than permanent occupation; however it is concluded here that the presence of human burials during the Lower Mesolithic occupational layers, in conjunction with the floral, molluscan and sedimentological evidence for multi-seasonal activity, would strongly suggest sedentary living (Cullen 1995; Runnels 1995). Occupation patterns gradually declined during the Upper Mesolithic, and by the last few centuries of the Mesolithic (Final Mesolithic), floral and faunal remains are extremely meagre, leading Perlès (2003) to suggest that occupation was limited to temporary stays (Hansen 1991; Perlès 2003).

The use of a cave as a permanent dwelling would have, to an extent, limited human exposure to *Anopheline* vectors. The cave itself could not have served as a shelter to the mosquitoes all year round; while high temperatures may have encouraged vectors to seek cool interior environments, the cold and damp conditions of the cave would not have been suitable for

winter hibernation. The occupants may therefore have escaped perennial transmission despite the viability of the climatic conditions.

Exposure during the warmer months may, however, have been high; the cave is suggested to have attracted vectors into the interior and it is hypothesised that the exploitation of the landscape during these periods would have heavily influenced the vulnerability of the occupants to malaria infection. The diet of the Mesolithic occupants indicates that much of their hunting and gathering was undertaken in areas of particularly high malariogenic receptivity (figure 4.6). The Palaeolithic diet, focusing largely on large game, gave way to a 'gathering' diet with an emphasis on marine resources during the Mesolithic. Large game disappeared from the faunal assemblage, perhaps due to the increase in woodland and the loss of grazing land to the marine transgression. These were replaced by a large range of smaller woodland animals that included *Cervus elaphus* (L., 1758) (deer), *Vulpes vulpes* (L., 1758) (fox) and *Sus scrofa* (L., 1758) (pig), which were hunted at the higher grounds and represent the largest of the Mesolithic prey. Smaller creatures were also targeted, such as birds, hares and *Erinaceus* (L., 1758) (hedgehogs), which were most likely hunted within the uplands and along the coastal plain (Payne 1975). Prolonged exposure to woodland habitats would have increased the vulnerability to the woodland fringe vector *A. maculipennis* and the exceptionally virulent woodland vector, *A. plumbeus.* The latter is known to be a persistent biter with strong anthropophilic tendencies, suggesting that this mosquito may have been a nuisance to the Mesolithic hunters.

The floral component of the Mesolithic diet appears to have centred on gathered goods often collected from areas with a potentially high malariogenic capacity; wild cereals were favoured, such as *Hordeum spontaneum* (C. L. Koch) (wild barley.), *Lens* spp. (wild lentils), and *Avena* spp. (wild oat) gathered from woodland, amongst the maquis, slopes and, in the

case of wild oat, amongst damp marshy ground (Hansen 1991). Other goods, such as nuts, fruits and bulbs are suggested to have been gathered from the stream incised valleys, banks of the streams and the coastal plain (Van Andel *et al.* 1987; Hansen 1991).

Environment *After Jameson et al.* 1994	**Resources** **Faunal** (Payne 1975)	**Floral** (Hansen 1991)	**Potential *Anopheline* vectors**
Coastal Zone: Rocky shores, shingle beaches, inlets, salt marshes, mud shoals	Rock dwelling molluscs, fish.	N/A	*A. sacharovi,* *A. superpictus,* *A. algeriensis,* *A. atroparvus*
Coastal Plain: Incised streams, grassland, and deciduous oak parkland.	*Cervus* (Red deer) small mammals, snails and birds	*Avena* spp. (wild oats), *Capparis* (caper) *Erodium* (storks' Bill), *Hordeum spontaneum* C. Koch. (wild barley), *Lens* spp. (lentils) *Prunus* amygdalus (almond), *Pyrus amygdaliformis* (wild pear) *Vicia ervilia* (vetch) *Vitis* (wild grape)	Mixed Habitats favouring all local *Anopheline* vectors
Stream banks and valley bottom: Open pine and oak parkland.	As for the coastal plain	As for the coastal plain and *Lathyrus* (Grass vetchling)	Mixed Habitats favouring all local *Anopheline* vectors
Upland Valleys and hills: Deciduous oak and pine woodland. Maquis.	*Cervus* (Red deer) *Sus* (Boar), small mammals.	*Pistacia* spp. (pistachio), *Prunus amygdalus* Batsch. (almond), *Hordeum spontaneum* C. Koch (wild barley), Malva (mallow) *Vicia* spp. (vetch) *Vitis* (wild grape),	Mixed Habitats favouring all local *Anopheline* vectors
Mountains; Dry, stony and barren slopes. Maquis.	N/A	*Pistacia* spp. (pistachio), *Prunus amygdalus* Batsch. (almond)	*A. claviger,* *A. plumbeus,* *A. sacharovi,* *A. superpictus*

Fig. 4.6. Resource bases during the Upper and Lower Mesolithic and the possible malariogenic capacity.

A notable emphasis was placed on marine resources with a considerable quantity of shell fish and molluscs being consumed, gathered from the cobble, gravel, and rocky environments along the coastal zone (Shackleton *et al.* 1986). Collecting such food types would inevitably entail considerable periods of time spent in, or at least alongside bodies of water, placing the gatherers in direct contact with extremely high volumes of fresh and brackish surface water in open landscapes which are strongly favoured by all the main *Anopheles* vectors.

It is suggested therefore that the Mesolithic occupants of Franchthi Cave would have increased their vulnerability to infection by the very nature of their economic activities; the amount of time spent hunting and gathering would be crucial in determining the rate of infection, however, this is an extremely difficult factor to determine from the archaeological record. Comparative studies with modern hunter-gatherer groups cannot be used as a 'definitive guide' to Mesolithic life but are, nonetheless, invaluable, as they provide the only direct observations of human behaviour in the absence of agricultural practices, and can aid interpretations with regards to the time-consuming nature of this economic behaviour. Studies of hunter gatherer groups from Africa, both sedentary and semi-sedentary, indicate similar amounts of time expended on food sourcing; foraging activities constituting on average c. 12-19 hours per week, while hunting is more time-demanding activity, constituting c. 24-32 hours per week (Sahlins 2004; Kent 2006), although this will naturally depend greatly upon the population size, the availability of resources and the distance of the resource base to the settlement. In the case of Franchthi Cave, it could be suggested that even an average of a few hours every day spent within areas of particularly high malariogenic capacity, for example, in proximity to areas of marshland or along the stream and river banks, would increase the likelihood of infection considerably. This exposure may have been increased further, as it has been suggested that much of the gathered food would have been consumed at the collection site rather than in the cave (Thomas 1987). Much of the diet was composed of gathered

resources such as plants, shell fish and molluscs, which carry an extremely high energetic cost compared to the hunting of large game; this would logically be minimised by immediate consumption. It may also increase the vulnerability of the foragers to malarial vectors even further if the collected foodstuff was consumed in proximity to malarious areas.

The environment of the coastal zone altered significantly during the Upper to Final Mesolithic period (figure 4.7), as a global rise in sea levels caused the coastal zone to be inundated. The marine transgression would have resulted in a propagation of *Anopheline* breeding grounds, as the coastline and the brackish water bodies along the coastline were gradually brought in closer proximity to the cave. An interpretation of the molluscan remains from Franchthi Cave indicate that by approximately c. 7550 BC (9500 BP)[82] the littoral zone lay at less than 2 km from the cave.

The presence of *Cerithium vulgatum* (Bruguière, 1789) (sea snail) within the faunal assemblage at Franchthi Cave indicates a large increase in shallow, brackish water while high abundances of the species *Cyclope neritea* (Risso, 1826) (dog whelk) and a substantial number of *Cerastoderma glaucum* (Poiret, 1789) (common cockle) indicate that open marshland developed (Shackleton *et al.* 1986). Thomas (1987) interprets this combination of species as characteristic of a marshy lagoonal habitat. A reconstruction of the shoreline from

[82] inferred from a dating curve based on sedimentation rates and seven secure radiocarbon dates:

	^{14}C yr BP	**cal. BP**	**Mean cal. BC**
Palaeolithic :	10,260±110	12018	10069
	9430±100	10690	8741
Mesolithic	9280±110	10470	8521
	9210±110	10399	8450
	9060±110	10221	8272
Neolithic	7981±106	8838	6889
	7929±101	8786	6837

(Shackleton *et al.* 1980). Calibrated with OxCal 4.1.

these studies indicates that areas of rocky shores and gravel beaches remained to the north and south of the site, while a small inlet, surrounded by open marshes and mud shoals, formed opposite the cave at approximately 1.5 km to the west (Shackleton *et al.* 1986).

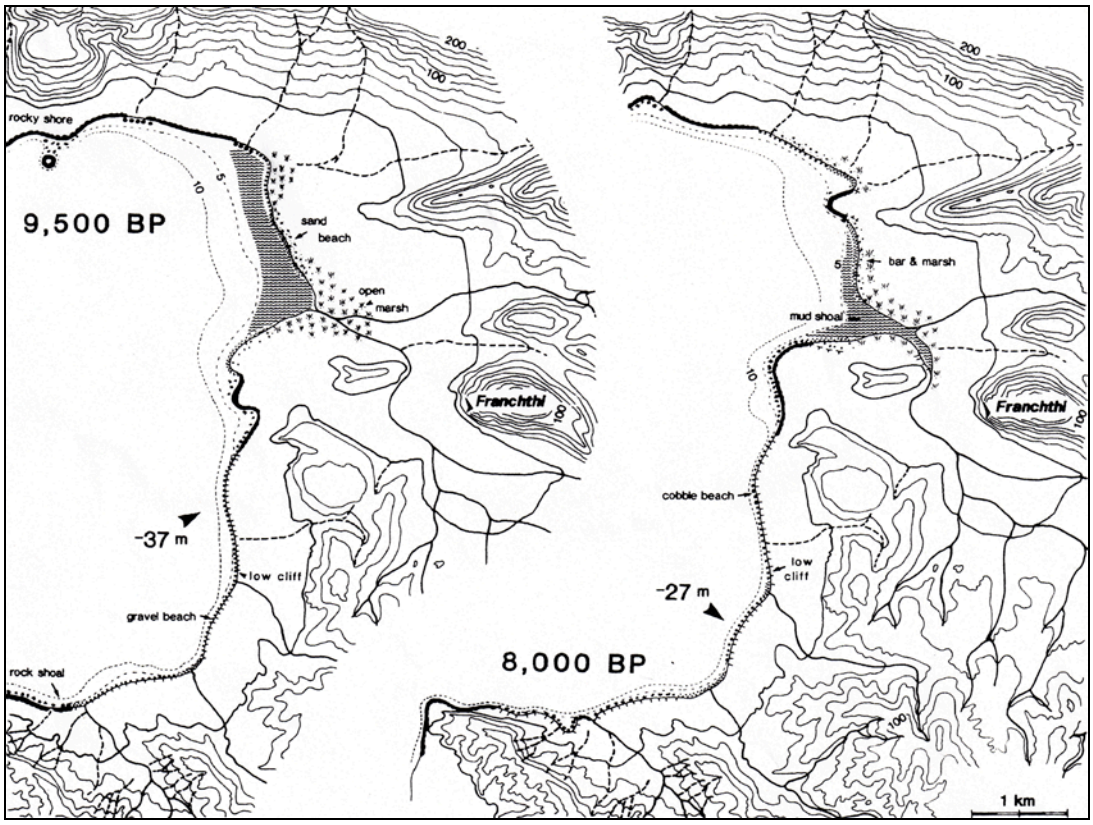


Fig. 4.7: The coastal environment of the Franchthi headland during the Upper Mesolithic (9500 BP) and Early Neolithic (8000 BP) (*After* Shackleton *et al.* 1986: fig. 10: pg. 138).

The development of marshland, volumes of shallow brackish water, combined with fresh water influxes from the continued and elevated flow of the Franchthi River, would suggest an abrupt increase in the malariogenic capacity of the littoral zone. It is suggested that only the most saline tolerant vectors, *A. algeriensis, A. atroparvus, A. hyrcanus* and most importantly the primary vector, *A. sacharovi* (Becker 2003), could have bred within the brackish and saline habitats; however, breeding grounds for the non-saline tolerant vectors would have

proliferated along the Franchthi River. Human exposure to these breeding grounds is suggested to have been high as the newly created marshland lay at less than 2 km from the cave, well within the flying distance of the *Anopheline* vector.

The faunal remains dating to this period furthermore indicate that the reliance on marine resources increased. *Thunnus thynnus* (L., 1758) (deep-sea blue fin tuna) constituted 95% of the fish remains and approximately 50% of the total faunal assemblage. This abundance was originally taken to indicate deep-sea fishing (Payne 1975) although this theory has recently been contested; scholars arguing, firstly, that the percentages were overestimated (Perlès 2003; Pickard *et al.* 2004) and secondly, that the tuna were more likely to have been caught by set net fishing from the shore (Rose 1994 cited in Perlès 2003; Pickard *et al.* 2004). This implies that the fishermen of the Upper and Final Mesolithic worked for long hours within a region with an exceptionally high malariogenic capacity; the more focused exploitation of this resource base may therefore have increased human exposure to malarial vectors.

The last few centuries of the Mesolithic occupation saw a severe economic downturn (Perlès 2003). Floral and faunal assemblages indicate a considerable reduction in resource exploitation, as the large scale fishing of the previous period disappeared, although it appears that the occupants continued to spend time gathering on the coastal zone, as only sea shells continue to be represented in any real quantity (Shackleton *et al.* 1986; Hansen 1991). The sparse occupational layers dating to the last few centuries of the Mesolithic naturally inhibits any robust interpretations on the nature or likelihood of malarial transmission, as the behavioural patterns of the population group are largely obscured. The suggested temporary nature of the occupation of the cave would indicate that exposure to the malariogenic capacity of the surrounding area would have been reduced.

The host group of Franchthi Cave is suggested to have been limited as there are few other Mesolithic sites in the region. Two find-spots (200-201), potentially representing one site, in the Kleisoura valley have been identified as a Lower Mesolithic site (Runnels 1996) and Koukou Cave, situated 5 km from Franchthi Cave has been dated to the Lower Mesolithic through lithic analysis (figure 4.8). The size of these sites, and therefore potential population sizes, has not yet been determined (Jameson *et al.* 1994). Zaïmis Cave, situated close to Megara in Attica, was occupied during the late Palaeolithic and possibly into the Mesolithic; however, there is little evidence for the population size and occupation patterns of this site (Galandiou *et al.* 2003b). Excavated during the 1920s by Markovits, the site is now destroyed and the published archaeological record is inconclusive (Perlès 1990).

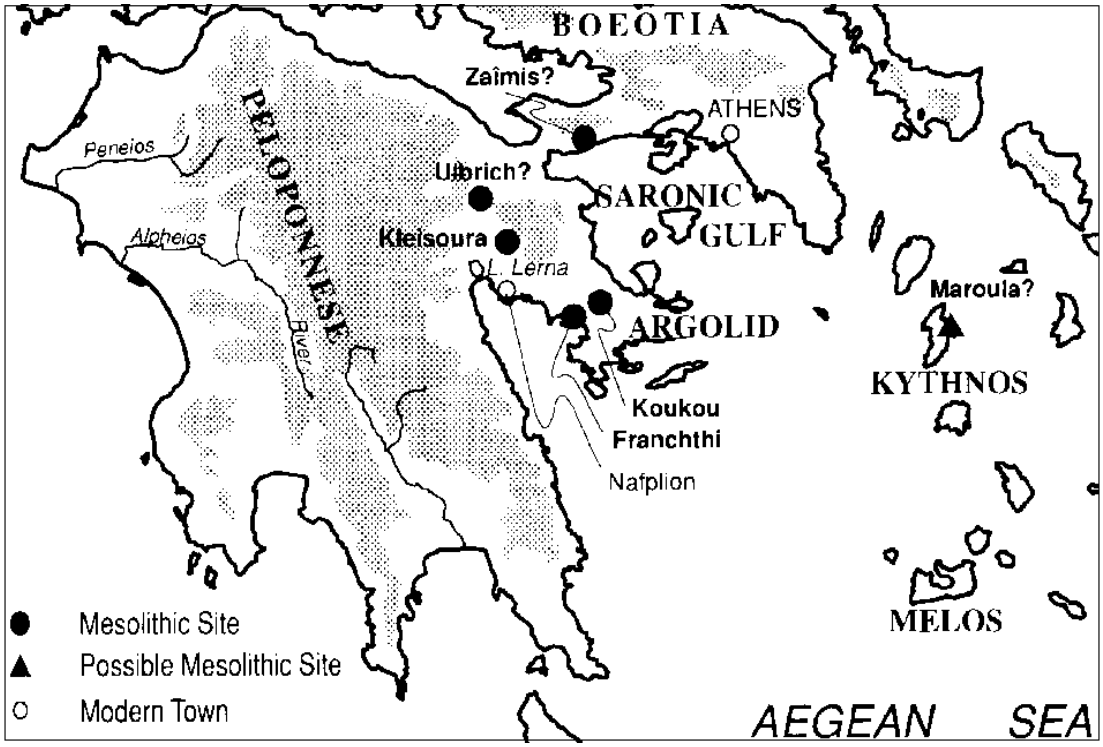


Fig. 4.8. Map of the Mesolithic sites of the Peloponnese (*After* Runnels 1995: fig. 9: pg. 721).

Finds from Ulbrich Cave indicate a Mesolithic and Neolithic occupational period; the significance of this site to the potential host group of the Southern Argolid is not evident as the archaeological data has been lost and even the exact location of the site is uncertain, although it is known to lie between Nemea and Nauplion. The lack of evidence pertaining to this site is unfortunate given the proximity of the cave to Franchthi; it has however been suggested that findspots 200-201 from the Kleisoura valley may in fact represent the 'lost' Ulbrich Cave (Runnels 1996). The evidence for Mesolithic occupation in the Peloponnese is therefore scarce; some scholars have argued that the lack of Mesolithic sites in the region is not due to low population densities but due to a loss of archaeological evidence through rising sea levels at the beginning of the Holocene (Runnels 1995; Séfériadès 2006). Regardless of the causes, the lack of evidence for other Mesolithic population groups obscures any conclusions as to the possible host group size and the implication for malarial transmission.

A reconstruction of the environment and palaeogeography of the area surrounding Franchthi Cave indicates a region of extremely high malariogenic potential during the Upper and Lower Mesolithic. The data indicate that all three *Plasmodiae* could theoretically have been introduced into the area during the beginning of this period and thrived, as ameliorated climatic conditions, high water availability and increasingly open landscapes would indicate a high malariogenic capacity. The stability of the Mesolithic climate is, perhaps, the most conducive element for malaria to have been both introduced and maintained. The increasingly favourable temperatures, augmented precipitation levels, lack of distinct seasonality combined with the mosaic of vegetation, varied topography, marshland and copious volumes of both fresh and brackish water, would have provided a multitude of varying and yet extremely viable habitats for the *Anopheles* vectors.

Interpretations of the behavioural patterns of both the Lower and Upper Mesolithic foragers would indicate that the population would have been susceptible to these malarial parasites, with the exception of the last few centuries of the Mesolithic when occupation of the cave was minimal. The hunters and foragers worked along the well-watered uplands, streams incised valleys, coastal plain and shore in close proximity to large bodies of water with high malariogenic capacity. It is suggested that the permanent or semi-permanent occupation of the region, especially during these periods of favourable climatic conditions, would further increase the vulnerability of the population to overlapping transmission seasons of the various sub-species, and therefore potentially to a high risk of transmission.

The Neolithic

The Neolithic at Franchthi Cave (figure 4.1) was a period of both climatic and environmental changes which coincided with the considerable social and economic transformations linked to the advent of agriculture. Dramatic alterations in economic behaviour, diet, population density and settlement patterns are evident in the archaeological record from Franchthi Cave; changes which are suggested to have the potential to radically alter the malariogenic capacity. These socio-economic factors, along with regional climate, microclimate and environmental conditions of the Franchthi headland will be considered from the beginning of the period until the Middle Neolithic in order to establish the malariogenic capacity of the region during this time frame. The different phases of Neolithic occupation will be dealt with separately due to distinct differences in the climatic trends (see chapter three), environmental changes and occupational patterns of these respective periods (Perlès 2001).

The Initial Neolithic (c. 7000-6450 cal. BC/ c. 8950-8400 cal. BP)

The occupation of Franchthi Cave during the Initial (or Aceramic) Neolithic appears to have continued in a similar manner to the final occupational phase of the Mesolithic (Perlès 2001). The local environment however underwent significant changes as the coastal zone continued to evolve; sea levels, steadily rising throughout the Mesolithic, had reached c. 10 m below the present sea level in c. 6550 BC (c. 8500 BP)[83] (van Andel *et al.* 1980; Shackleton *et al.* 1986). This transgression reduced the coastal plain so that the cave overlooked a narrow strip of coastal meadow.

Although precise dating is not possible, sediments from cores taken from the shore of Franchthi indicate a second alteration to the coastal zone when a barrier formed off the coast shoreline between c. 7050 BC and 6050 BC (9000/8000 BP); perhaps having developed through accumulation of sand due to alluvial deposits from the Franchthi River, this barrier enclosed the estuary and may have persisted until c. 4050 BC/ 6000 BP (van Andel *et al.* 1980) (figure 4.7). *Cerithium vulgatum* is the dominant bivalve in the faunal assemblage between c. 7450-6550 BC (9400-8500 BP)[84] which Shackleton (*et al.* 1980; *et al.* 1986) suggest reflects the development of a shallow inlet. This would therefore suggest that the coastal environment dating to 8000 BP, shown in figure 4.7, occurred during the Initial Neolithic.

The shallow waters of this inlet would ostensibly have remained brackish, although sedimentological studies suggest that the perennial Franchthi River that bisected the plain would have fed into this inlet, which may have introduced fluxes of fresh water into the

[83] c. 7705±14 ^{14}C yr BP (Reimer *et al.* 2004). These inferred dates are based on the general eustatic sea level curve and supplemented by bathymetric data. The projected curve concurs with ^{14}C dates provided by Kraft *et al.* 1975.
[84] See note 82 for dating methods of this faunal assemblage.

environment (van Andel *et al.* 1980). The enclosed inlet further promoted the formation of a deep slough (a stagnant swamp, marsh or bog) within the river valley leading to the bay; this is suggested to have formed at less than 1 km distance from Franchthi Cave (van Andel *et al.* 1980).

The changes to the coastal zone during the Initial Neolithic would indicate a gradual but significant expansion in viable breeding grounds for most of the *Anopheline* vectors. The marshland, shallow brackish water and the high volumes of fresh water introduced from the Franchthi River would suggest a high volume of varied breeding grounds for both the saline and non-saline tolerant vectors. The fluctuating quality of the water from the inlet may have occasionally, or perhaps seasonally, caused the water body to become suitable for all the local vectors. Modern malaria studies show that ecological changes that predominantly favour certain vectors over others can result in competitive displacement, causing the population density of the sub-species to augment and potential infection rates to rise (Lounibos 2007). At less than a kilometre distance from Franchthi Cave, these marshy areas and lagoonal habitats are suggested to have presented a particular threat to the Initial Neolithic occupants, lying within the flight range of the *Anopheline* vectors.

The environmental disturbances were not the only element to disrupt disease patterns during this period. The Initial Neolithic saw the introduction of new socioeconomic elements, not just at Franchthi Cave but to the Greek mainland as a whole. This immense event in human history is suggested to have been linked to migrations from the Near East; the 'demic diffusion' or 'wave of advance' theory (Ammerman *et al.* 1971; 1984) suggests that populations moving west brought new crop seeds and the knowledge of domesticated animals to the Aegean, sparking the Neolithic 'agricultural revolution' (Perlés 2001). This theory has been strongly debated in recent years as scholars have argued against this 'diffusionist'

theory, preferring an 'indigenist' explanation, asserting that these new socio-economic elements developed locally (Theocharis 1973b). The wave of advance theory is now supported by recent aDNA studies (King *et al.* 2008; Chikhi *et al.* 2009); Y-chromosome data indicates that while populations from mainland Greece (Nea Nikomedeia, Sesklo and Dimini) show a greater affinity with Balkan populations, the Initial Neolithic occupants from Franchthi Cave are grouped with those from Crete and Anatolia. This would suggest a "regional interaction between Crete, the Peloponnese and Anatolia", supporting a theory of 'foreign' contact (King *et al.* 2008: 211).

It appears that despite the introduction of new material cultural elements, the material culture is a definite continuation from the previous period (Hansen 1991; Perlès 2001). Perlès (2001) therefore suggests that the new cultural and economic elements within the assemblage reflect contact and exchange with new groups from the Near East, rather than an immediate absorption of a new population into the group, or an invasion of a new culture. It is suggested, based on correlations with modern malaria studies, that the vulnerability of both local groups and migrant groups to malaria would have been increased by exposure to these foreign population movements. Historical examples show that trade and contact with foreign cultures can have an extremely strong influence on the spread of disease, potentially initiating epidemic outbreaks when populations travel from a non-malarious area into an affected region (see chapter two) (Prothero 1977; Martens *et al.* 2000).

The modifications to economic behaviour, the landscape and social organisation during the Initial Neolithic were considerable, and it is suggested that these changes would have had strong effects on existing disease patterns. The introduction of new technologies is also suggested to have increased the malariogenic capacity of the landscape; modern malaria studies indicate that the early cultivation of crops, the associated land clearance, soil

disturbance and the domestication of animals, would have augmented the malariogenic capacity of the area and increased the agricultural workers exposure to the *Anopheline* vectors (see chapter two) (Patz *et al.* 2000; Pattanayak *et al.* 2008).

An interpretation of the environmental lifestyle and economic behaviour of the Initial Neolithic is difficult, as the occupational layers of this period are unfortunately extremely poorly represented having been disrupted by subsequent periods of activity within the cave (Hansen 1991; Perlès 2001). The occupation of the cave appears to follow a similar pattern from the final centuries of the Mesolithic. The living quarters within the cave were restricted to just one area and Payne (1975) notes a paucity of faunal remains. A very low sedimentation rate of 8 cm per 100 years indicates far less intensive occupation pattern than that of the Lower Mesolithic where 250 cm of sediment were deposited per 100 years (Farrand 2000). This may suggest that the population was semi-permanent and perhaps that the cave was used as a satellite herding camp (Payne 1975). The floral remains may, however, indicate that a considerable percentage of the year was spent at the cave; the sowing and harvesting patterns linked to *Triticum turgidum* spp. *dicoccum* (Schubl.), (domesticated wheat), *Hordeum vulgare* spp. *distichum* (L.) (two-row barley), legumes and pulses would suggest year round agricultural activity (Hansen 1991). The emergence of emmer wheat and two-row barley, may equally indicate that crop seeds were being traded with the migrant groups or with other Neolithic settlements where farming had already begun (Hansen 1991; Perlès 2001). There is therefore too little evidence to draw any conclusions as to the exact patterns of occupation; it will be assumed here that the cave was not used as perennial dwelling, but was periodically abandoned. It is also noted that no other Initial Neolithic settlements have been identified in the locality and the extent of local contacts cannot be determined.

As farming activity is not securely identified until the Early Neolithic, the malariogenic potential linked to such activities will be discussed below. Macrobotanical remains from the cave appear to reflect some economic continuity from the previous period, as wild plants continued to be exploited from the valleys, stream banks and coastal plain. The faunal diet altered significantly during the Initial Neolithic, as the proportion of wild fauna within the assemblage decreases significantly in favour of domesticated fauna. An abundance of ovicaprids is recorded, with *Ovis aries* (L., 1758) (sheep) representing 90% of the total sample. *Capra hircus* (L., 1758) (goat) remains were present among the assemblage of the preceding periods and their presence is therefore not as remarkable, except for their new domesticated role; sheep, however, were not native to the area and are suggested to be another indication of an intruding culture (Payne 1975; 1985). Small birds and fox continue to be hunted, remains of pig and deer are scarce, tuna remains are entirely absent and cattle do not reappear in the assemblage until the Early Neolithic, indicating a significant shift in economic behaviour (Payne 1975; 1985; Perlès 2001). The time previously spent hunting and gathering was instead spent herding the newly domesticated flocks to and from grazing pastures, presumably amongst the maquis and grassland, found along the stream and river sides, valley floors, and along the coastal plain, where there would be easy access to drinking water. The occupants were, therefore, still working amongst areas with high malariogenic potential.

The introduction of domesticates could have further altered transmission patterns as the landscape can change in response to grazing. While goats will graze on scrubland, often favouring slopes and areas of maquis, sheep require considerable areas of grazing land; farmers will therefore either create small clearings in order to sustain their flocks or will exploit natural open grasslands, valley floors and stream banks such as those that surrounded Franchthi Cave. There are, unfortunately no local pollen cores dating to this period and there

is therefore no evidence for anthropogenic land clearance (Hansen 1991). It is, however, unquestionable that these animals had access to grazing and it is well recorded that browsing animals will maintain and even expand open areas of land by constant cropping of the surrounding vegetation; Grove (*et al.* 2001) argues that consistent animal browsing will not degrade the landscape but will alter the nature and composition of the vegetation, often promoting the growth of phrygana, and other low shrub communities.

Changes to the landscape, even if on an extremely small scale, will alter the microenvironment and therefore the malariogenic potential of the area. The maintenance or expansion of open land will favour many of the most efficient of the suggested vectors; for example, areas of vegetation along the stream banks would have been cleared by grazing livestock seeking drinking water, and the suitability of water body as breeding grounds would have altered accordingly. The removal of overhanging vegetation or shrubs which produce shade would cause the pool or stream to become sunlit and the temperature of the water to increase, favouring some vectors such as *A. sacharovi* and *A. superpictus* and decreasing the prevalence of others (Lividas *et al.* 1941). The favoured vectors will therefore flourish and the populations can often expand exponentially. This would constitute a particular threat if the species is an efficient vector or persistent biter (Lindsay *et al.* 1996; Yasuoka *et al.* 2007). Studies have noted that epidemics can be linked to vector abundance rather than just efficiency; a relatively innocuous vector can maintain a high malarial burden if the population density of the said vector is sufficiently high (Beljaev 2002). An environmental change in favour of any of the *Anopheles* of the locality would then have potentially resulted in an increased malarial burden.

The density of the *Anopheles* may also have been augmented by an increased volume of breeding grounds due to the grazing ovi-caprine; animal footprints, once filled with water, are

recognised as a preferred breeding ground of vectors which favour still waters; such as *A. sacharovi* and *A. maculipennis* (Lividas *et al.* 1941; Bruce-Chwatt 1980). This would of course have been a factor even before the domestication of animals, due to the presence of wild animals; however, regular movements of the ovi-caprine herds would undoubtedly have augmented the frequency of such breeding grounds. It is suggested that the risk of infection associated with the care of these ovi-caprine herds was high, not only due to the increased malariogenic capacity of the environment, but also as the most active periods of animal husbandry, including spring breeding and grazing during the warmer months would coincide with the peaks in the *Anopheline* populations.

The domestication of animals may have had yet further consequences to disease patterns; the discovery of deciduous ovicaprid milk teeth within the very earliest occupational layers of Franchthi Cave dating to this period led Payne (1985) to suggest that the newly domesticated flocks may have been stabled within the cave. This would appear a logical choice, serving to both protect the flocks from predators without having to construct specific pens, and to increase the temperature within the dwelling, helping the human inhabitants to keep warm (Lindsay 2002; Ye *et al.* 2006). Adult mosquitoes will actively seek shelter at the heat of the day and during cooler months, favouring houses and animal shelters as they provide food and warmth; sufficiently warm indoor temperatures can induce partial hibernation, prompting the vectors to feed throughout the winter, again putting the occupants at increased risk of infection. The microclimate of the dwelling, the indoor temperature, humidity and the nature of ventilation, will affect vectors behaviour; suitable indoor conditions can result in extended transmission seasons and increased infection rates as mosquitoes are protected from the unfavourable elements (Shannon 1935; Garnham 1948). The combination of humans and stabled animals would augment the heat of the indoor environment; combined with the

presence of food and the inherent humidity, the cave is therefore suggested to have been particularly attractive to vectors during the colder months (Garnham 1948).

Infection rates may have been altered by the practice of stabling animals within human dwellings; the theory of zooprophylaxis suggests that the presence of animals may detract the vectors away from the human occupants (WHO 1982). The consequences of this zooprophylaxis are, however, difficult to define, as some studies have shown that the practice may in fact increase the infection rate, as the 'host odours' exuded by the animals can attract greater numbers of vectors to the domicile, while the readily available blood provided by the animals can increase vector density and survival rates (Bouma *et al.* 1995; Saul 2003; Killeen *et al.* 2004). The efficacy of zooprophylaxis furthermore depends on the species of animal stabled; sheep, goat and pig have been shown to be far less attractive than cattle to zoophilic vectors (Lividas *et al.* 1941). The stabling of the former species within the cave may therefore have increased the frequency of vectors within the cave but only detracted a minimal percentage away from the human population, thereby increasing the malariogenic capacity of the locality.

The changes to the coastal zone and anthropogenic influences on the landscape of the Franchthi headland during the Initial Neolithic period appear therefore to have increased the malariogenic capacity of the environment, suggesting that the potentially suppressive effects of the climatic deterioration at c. 6850/6650 cal. BC (8800/8600 cal. BP)[85] on malaria transmission (see chapter three) may have been mitigated. The gradual decline in temperatures and humidity levels which persisted throughout this period is likely to have been alleviated by the expanding human populations, the potential for hibernation within the

[85] 7986 ± 17 ^{14}C yr BP -7840 ± 15 ^{14}C yr BP (Reimer *et al.* 2004)

human dwellings, the introduction of domesticated livestock and their influence on the landscape and incipient agricultural activities. It is suggested that the social and economic developments of the Initial Neolithic would have increased the malariogenic capacity of the environment and therefore the vulnerability of the populations to infection, despite the gradual climatic deterioration.

The Early Neolithic (6450-5900 cal. BC/c. 8400-7850 cal. BP)

Excavations of the Early Neolithic occupation levels (figure 4.1) indicate very little continuity from the previous occupation levels. Analysis from the cave indicates a prolonged gap in sediment deposition between c. 8500 and 8000 BP, leading Farrand (2000) to propose a five hundred year occupational hiatus between the Initial and Early Neolithic. Ceramic evidence would tentatively support this contention, suggesting a "possible…[…]... hiatus in site use", however the period of abandonment is not suggested to have been as extended as the sediment analysis indicates (Farrand 2000; Vitelli 1993: 39). The distinct alterations to the material culture linked to the reoccupation of the site have led Demoules (*et al.* 1993) and Perlès (2001) to suggest that a culturally distinct group had migrated into the area. The migrating populations introduced many socio-economic practices as new crops, domesticated animals and agricultural techniques emerge in the archaeological record.

A notable feature of both the Early and Middle Neolithic is the increased number of settlements that emerged across the north-east Peloponnese; the development of several substantial sites within the Argive Plain and identification of multiple settlements in surveys of the Nemea valley and Berbati-Limnes region (figure 4.9) indicate a considerable expansion in agricultural settlements. The sites, varying in size from less than one hectare (Nemea findspot 201 and Berbati findspot 400) to 4 hectares (EN-MN Corinth), would suggest a considerable population increase and, by extension, an increased host group for the

malaria parasites (Wells *et al.* 1990; Wright 2004). There is, however, an absence of evidence for permanent sites within the Southern Argolid (with the exception of Franchthi Cave) until the Middle Neolithic period; a survey of the region identified one MN site, Mouzaki Cave, on the east coast (Demoules *et al.* 1993; Jameson *et al.* 1994).

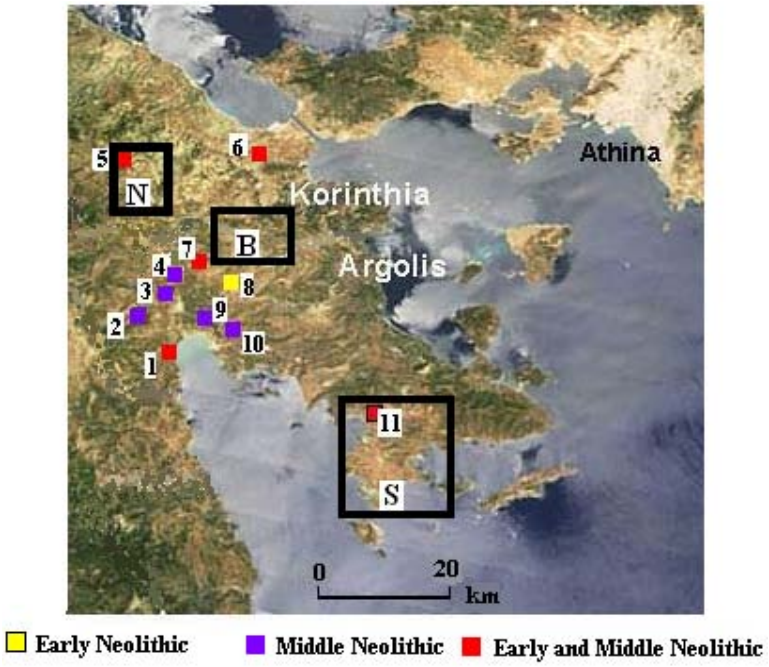


Fig. 4.9. Map of Early to Middle Neolithic sites and three survey areas in the Peloponnese and Southern Argolid.

Key: N: Area of Nemea Valley Survey: 4 EN sand two MN sites. **B:** Area of Berbati-Limnes survey: 1 EN and two MN sites. **S:** Area of Southern Argolid survey: one MN site. **1.** Lerna **2**. Kephalari Cave **3**. Argos **4**. Prosymna **5.** Philus **6.** Corinth **7**. Mycenae **8**. Dendra **9**. Tiryns **10.** Aria **11**. Franchthi Cave (Wells *et al.* 1990; Jameson *et al.* 1994; Johnson 1996; Wright *et al.* 2004).

It has been suggested that this lack of sites may reflect a different pattern of landscape exploitation, perhaps seasonal movements or a loss of evidence due to subsequent sea level rises (Runnels *et al.* 1987; Demoules *et al.* 1993). Despite the lack of local sites within the Southern Argolid, it is proposed that the proximity of the Franchthi headland to the more

densely populated Peloponnese, coupled with the suggested development of transhumance practices, would indicate a highly expanded host group.

Expanded trade networks may have increased this host group further, potentially causing the introduction of the disease to a previously unaffected group of people (Martens *et al.* 2000). Evidence of traded or exchanged goods with outside groups during this period is plentiful in the archaeological record. Excavations revealed marble, Melian obsidian, a honey-coloured flint that may be from Bulgaria, Aiginetan andesite and carnelian beads; the presence of these objects suggest that contact with other population groups was a regular occurrence (Jacobsen 1981; van Andel *et al.* 1988; Perlés 2003) and it is therefore hypothesised that the potential for the success of *P. falciparum* during the Early and Middle Neolithic is greater than that of the preceding periods.

The transition between the Initial and Early Neolithic at Franchthi Cave saw the establishment of a permanent settlement, as the site expanded onto the Paralia, a narrow terrace directly in front of the cave (figure 4.10) (Jacobsen 1969; Perlés 2003). A substantial settlement of sturdy rectangular houses was built overlooking the coastal plain, facing the steadily encroaching inlet and the open marshes as indicated by the coastal reconstructions (van Andel *et al.* 1980; Jacobsen 1981). Much of the Paralia is now obscured by subsequent sea level rises; however, marine sediments from the modern shore line indicate that the settlement extended over one to two hectares or more (Wilkinson 1990), spreading from the terrace in front of the cave towards the now submerged Franchthi River (van Andel et al. 1980).

The suggested spatial extent of the site allows an estimation of the population size, although this exercise is clearly not without its difficulties. Models vary considerably; Halstead suggests a model of 100 people per hectare (1981), while Renfrew has estimated

approximately 200 per hectare (1972). Regardless of the accuracy of such estimates, it is evident from the construction on the Paralia that the settlement had become significantly more substantial. The construction of permanent houses would not only indicate continuous occupation, but would also alter adult vector behaviour by providing suitable shelter for both resting and hibernating. The walls of the houses were constructed of stone, the cracks in which would not offer much protection against *Anopheles* vectors; these may have been filled in with a mud daub mixture, as has been noted in other Early Neolithic settlements such as Nea Nikomedeia, Sesklo and Argissa[86] (Milojčić *et al.* 1962; Rodden 1964; Theocharis 1973b) as an aid to insulation, which would help reduce the accessibility for the vectors (Lindsay *et al.* 2002; Ye *et al.* 2006). This is entirely hypothetical as there is no evidence for any other building materials (Jacobsen 1981) and the vulnerability of the inhabitants to nocturnal infection cannot therefore be ascertained. However, the position of the site, in close proximity to the coast, marshes and the springs (see figure 4.7) would suggest that nocturnal vulnerability was fairly to extremely high during the warmer months.

The introduction of new technologies during this period would have been a major contributing factor to the malariogenic capacity of the area. The introduction of arable farming and new crops would have required extensive environmental alterations, such as land clearance and tillage of the soil, which would have resulted in a concomitant increase in the malariogenic capacity of the area. Ethnoarchaeobotanical remains from Franchthi Cave indicate that the inhabitants began to clear and cultivate the land around the cave; *Coriandrum sativum* (L.) (coriander) appears in the macrobotanical record, indicating disturbed land, while field weeds increase in volume indicating the presence maintenance of open, arable land (Hansen 1991).

[86] The former two are Macedonian settlements, while the latter is located in Thessaly.

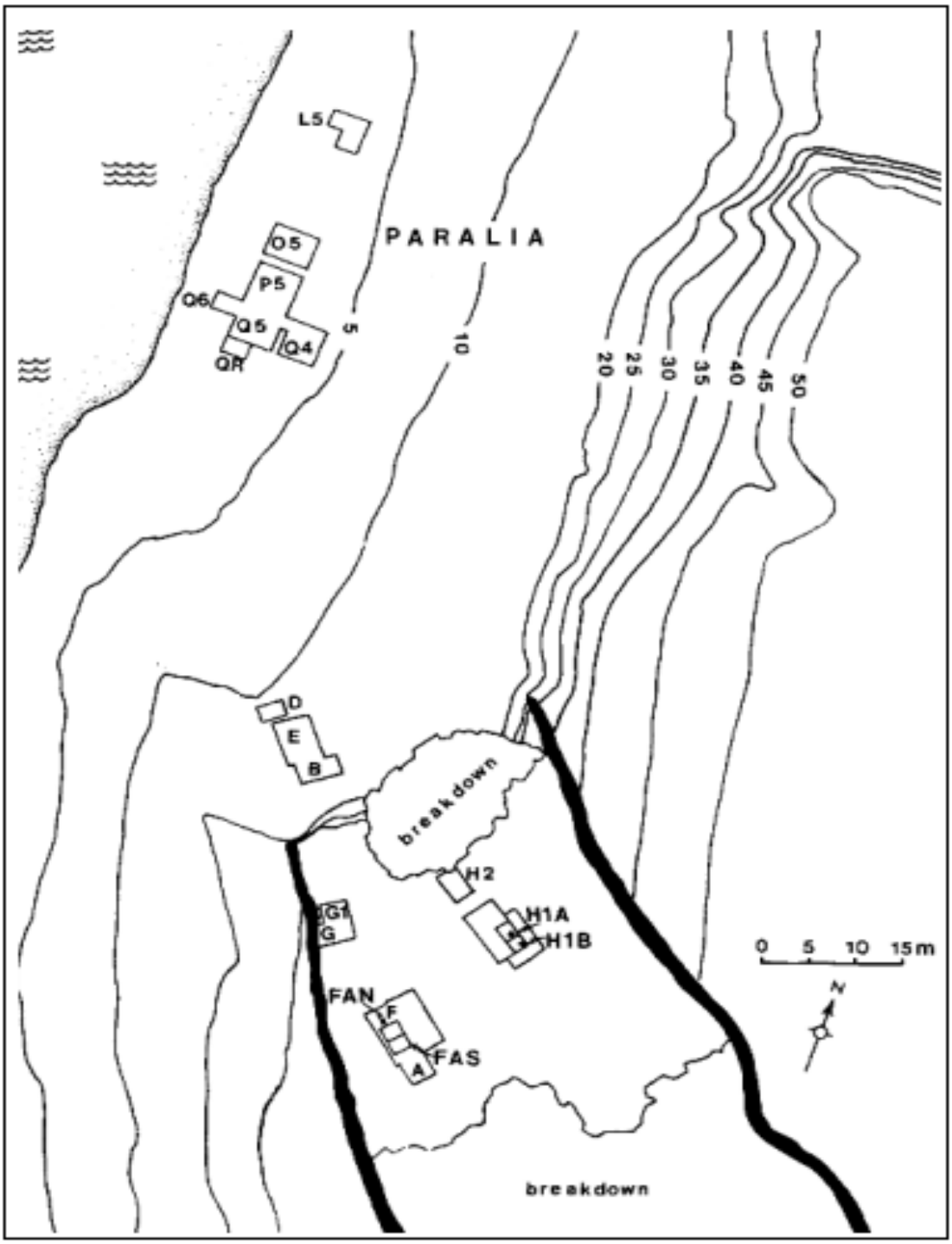


Fig. 4.10. Excavation plan of Franchthi Cave (outlined in black) and the Paralia (*After* Shackleton *et al.* 1988; fig. 2: pg. 7).

Newly introduced domesticated crops and cereals, including emmer wheat, two-row barley, *Lens culinaris* (Medik.) (cultivated lentil) and vetch, are suggested to have been cultivated on the spring-fed meadows in front of the Paralia, which would have been extremely fertile and would have provided a small but reliable yield (Hansen 1991; van Andel *et al.* 1988). Small scale clearances such as those hypothesised would have strongly affected the micro-climate by altering humidity and temperature, thereby affecting vector distribution (Patz *et al.* 2000). The identification of these crops and of land clearance further indicates the suitability of the soils for malarial reproduction; the absence of tree cover will firstly result in sunlit water bodies which favour the primary vectors. Secondly, the absence of organic humus produced by tree cover can increase the pH level of the soils to neutral rather than acidic levels, which create far more favourable *Anopheline* breeding grounds and will actively encourage breeding (Patz *et al.* 2000; Kampen *et al.* 2004). The pH levels of the area are likely to have been neutral to base given the predominance of limestone in the Southern Argolid and this is tentatively confirmed by the pH tolerances of the crops mentioned above; the average of which requires between pH 7-8 to grow adequately (Oplinger *et al.* 1989). These pH levels correspond to the optimum pH levels for *Anopheline* oviposition; *A. maculipennis*, *A. superpictus* and *A. claviger*, for example, actively seek water bodies with a 7.64-7.88 pH level (MacGregor 1929; Kampen *et al.* 2003). The early farmers were therefore creating or at least exploiting highly viable malaria breeding grounds as streams, puddles or even footprints filled with water around the cultivated area would have been ideal breeding grounds for all vectors favouring sunlit water bodies.

The suitability of the soils to malaria breeding grounds would have been exacerbated further by the high volume of both fresh and brackish water from the springs, marshes and the encroaching inlet which lay in close proximity to the newly cultivated areas. This would indicate that the farmers would have had a high risk of infection; it was undoubtedly a risky

profession as seasonal activities related to the crops would, like animal husbandry, coincide with peaks in vector population sizes. *Hordeum* and *Triticum* would have been sown during the autumn and harvested during the spring, while the legumes and pulses would have been sown during the spring and harvested during the late summer to early autumn (Hansen 1991). Agricultural labouring would therefore coincide with the height of the malarial season and the various population peaks of the local vectors; given the malarial capacity of the environment in which the Neolithic farmers worked, it is suggested that the risk of infection was potentially high.

The occupants therefore largely focused on domesticated crops and domesticated animals, the latter increasing considerably in frequency during the Early Neolithic. Cattle and pig appear in greater quantities; however the emphasis remained upon ovicaprids herds (Payne 1975; 1985). The sea shore was also frequented, as the assemblage indicates that the diet of the early farmers was supplemented by fishing and shell fish (Payne 1975). Worked shell became prevalent; quantities of *Spondylus gaederopus* (L., 1758) (spiny oyster), *Mytilus galloprovincialis* (Lamarck, 1819) (salt and fresh water mussels) and *Luria lurida* (L., 1758) (cowrie) were found, suggesting that the occupants were still spending time along the coastal pools, open marshes and the inlet (Jacobsen 1973). Labouring hours were spent, as during the Initial Neolithic, herding and foraging within regions of considerable malariogenic potential.

The malariogenic capacity of the Early Neolithic environment is therefore suggested to have increased further as a result of growing populations and expanding anthropogenic influences; however, this period coincided with the abrupt climatic deterioration of 6250 cal. BC (8200 cal. BP)[87] which would have limited this capacity (Rohling *et al.* 2002; Geraga *et al.* 2005). The c. 200-300 year decrease in winter temperatures and humidity levels would have

[87] 7400/7500 ^{14}C yr BP (Alley *et al.* 1997).

prevented the sporogonic cycle from completion and the *Anopheles* from remaining active during the cooler months. The possibility of hibernation during the winter months, which would have been promoted by the construction of permanent dwellings, is unlikely to have alleviated the effects of a 2-4°C decline in temperature sufficiently to support perennial transmission (Rohling *et al.* 2002; Gougou *et al.* 2006; Kotthoff *et al.* 2008). Summer temperatures and humidity levels were, however, unaffected (Rossignol-Strick 1995) and, combined with the increasing malariogenic capacity of the environment, this may have promoted seasonal transmission, indicating a potential for more intense infection patterns.

The inherent malariogenic capacity of the landscape would have been increased considerably by the changes to the economic and social activities of the local population. The introduction of a settled farming economy, including the introduction of permanent dwellings, land clearance and cultivation and domestication of animals would have increased the risk of infection during the summer months considerably by irrevocably altering vector habitats and behaviour and, as a consequence, malaria patterns. In effect, the developments of the Early Neolithic caused the vector populations to adapt for the first time to a human influenced environment, as farming created new breeding grounds, human dwellings provided favourable warm shelters, and domesticated animals increased the attraction of the site and, for some vectors, the food sources. These are all factors which would have the potential to increase biting behaviour, longevity, abundance and exposure. It is not suggested that malarial infection would have been ubiquitous; the small populations and consequential limits on anthropogenic clearance would have undoubtedly tempered infection rates. The climatic and environmental conditions of the Franchthi headland may therefore have exposed the populations of the Paralia to a high, but seasonal, malariogenic capacity, which may theoretically have resulted in more intensive transmission patterns.

Middle Neolithic (5900-5300 cal. BC/ 7850-7250 cal. BP)

The coastal environment of the Franchthi headland appears to have remained stable throughout the Middle Neolithic (figure 4.1); however a pollen core from the now submerged Franchthi River in Kiladha Bay permits a reconstruction of the vegetation cover which appears to have altered considerably. The beginning of the pollen core is contemporary with the mid to late Middle Neolithic[88]; while the early phase of the Middle Neolithic is not represented, the later phases may be considered as a fair reflection of the earlier landscape.

Analysis of the pollen core indicates a very open, steppic landscape. Arboreal pollen is low (30%), and is largely represented by deciduous and semi-deciduous oak. *Pistacia* pollen value is exceptionally high at 3%, while lime, hazel and elm are also well represented (figure 4.11) (Bottema 1990). *Gramineae* values are low, which Bottema (1990) suggests may either indicate heavy grazing or that grass was a minor element of the Franchthi headland landscape; the latter explanation is favoured. Halophytic (salt-tolerant) taxa, such as Chenopodiaceae and *Liguliflorae* are also extremely frequent within the core, reflecting the proximity of the sea to the river channel (Bottema 1990). The landscape surrounding Franchthi Cave is therefore suggested to have been one of open steppe with limited vegetation cover; *Tilia, Corylus* and *Ulmus* are suggested to have grown along the north slopes and the stream valleys, while *Pistacia* and herb taxa would have covered the low elevations (Bottema 1990).

[88] The Kiladha Bay core produced three radiocarbon dates (Bottema 1990). Calibrated with OxCal 4.1 to σ2.

^{14}C yr BP	**Cal. BP**	**Cal. BC**
6860±120	7941-7509	5992-5560
6720±100	7757-7428	5808-5479
6600±250	7958-6960	6009-5011

Macrobotanical remains from the Middle to Late Neolithic occupation would support this interpretation of a more open landscape; frequencies of *Pistachia, Prunus* and *Pyrus* decrease substantially in the floral assemblage, which could be the result of land clearance across the hills and valley floor, potentially for agricultural purposes. It is worth noting that these areas are still considered prime for crop cultivation (Hansen 1991).

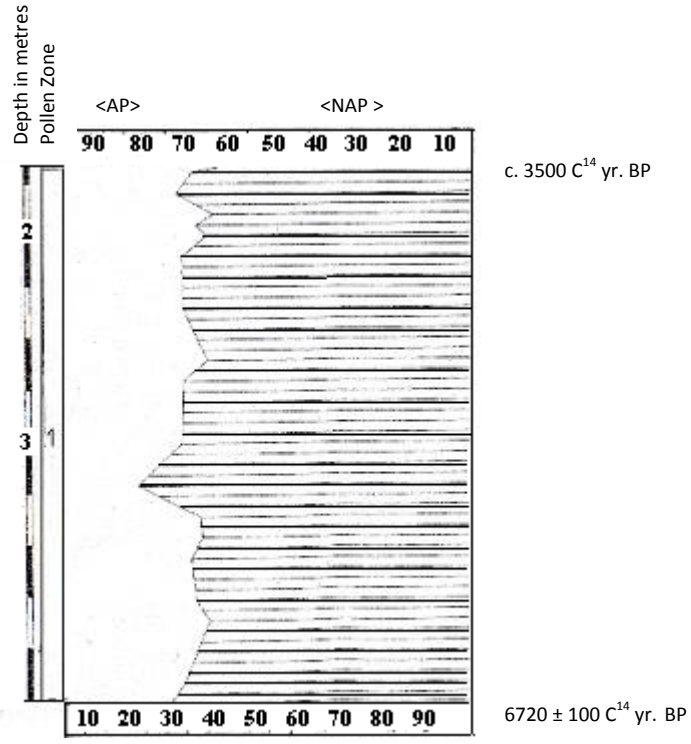


Fig. 4.11. Pollen core from Kiladha Bay showing Arboreal/non-arboreal pollen. The termination of pollen zone 1 is based on sedimentation rate of 0.7 mm/yr. and comparisons with other pollen cores (*After* Bottema 1990; fig. 47: pg. 121). Modified by author.

This would indicate a landscape which is contrary to predictions of heavy forest cover; rather than the landscape precluding the 'tropical' *Anopheline* vectors from the Aegean (Bruce-Chwatt *et al.* 1980; de Zulueta 1994), the pollen data from Kiladha Bay would in fact indicate a highly receptive landscape. The open steppic environment with minimal forest cover would

suggest that habitats of both *A. sacharovi* and *A. superpictus* would have been highly prevalent (Becker 2003). The capacity of the environment may have been exacerbated further by the increasing anthropogenic activity evident in the pollen record. Bottema (1990) noted large quantities of charcoal within the core, which would indicate land clearance by fire; an explanation which is further supported by high values of cereal pollen and field weeds such as *Asphodelus* (L.), which is common in ploughed fields and may suggest an expansion of the field systems (Bottema 1990). Grazing pressure is also evident; *Plantago lanceolata* (L.) (ribwort plantain), *Poterium* (L.), (burnet), *Mercurialis annua* (L.) (annual mercury) are fairly well represented in the pollen record, all of which profit from anthropogenic influence (Bottema 1990).

This episode of anthropogenic land clearance is suggested to have increased the malariogenic capacity further; modern studies of slash and burn techniques in tropical areas have shown a strong link between this agricultural practice and higher incidences of malaria, as not only does it reduce tree cover, therefore favouring the sunlight-loving primary vectors, but it will also reduce the number of vector resting places (Patz *et al.* 2000; Klinkenberg *et al.* 2004). Many vectors, even those that favour sunlit rather than shady areas such as *A. sacharovi* or *A. superpictus*, will seek areas such as tree trunks in order to rest during the hotter hours of the day.

Burning or clearing woodland can reduce these areas, forcing the vectors into other shelters, often human dwellings, which inevitably increases the risk of infection (Klinkenberg *et al.* 2004). Furthermore, the removal of tree cover will alter the ecosystem (see chapter two), affecting population density, reproduction rates, longevity and the availability of suitable breeding grounds (Patz *et al.* 2000; Yasuoka *et al.* 2007). With regards to the vectors of Greece, the open landscape, land clearance and increase in grazing pressure would have

limited the dispersal of the forest dweller, *A. plumbeus*, and mosquitoes that breed in partially shaded water bodies, such as *A. maculipennis*, while sun-seeking vectors would have been highly favoured (Lividas *et al.* 1941; Becker *et al.* 2003; Yasuoka *et al.* 2007).

High frequencies of cerealia pollen within the pollen core from Kiladha Bay indicate that the crops were sown, or more likely threshed, extremely close to the coring site (Bottema 1990). This would indicate that the farmers worked in close proximity to the now-submerged river; the fresh water, combined with the saline water, as evidenced by the high frequencies of halophytic taxa, would suggest that the Middle Neolithic farmers worked in close proximity to multiple breeding grounds, suitable for both local and 'tropical' vectors. Vulnerability to infection may therefore have been high (Le Menach *et al.* 2005).

Archaeological and palynological evidence further indicates an increase in animal exploitation during this period which may have boosted the malariogenic capacity. The faunal and pollen evidence for a greater emphasis on domesticated animals is supported by the large quantities of spindle whorls and loom weights dating to the Middle Neolithic assemblages, which indicate the increasing importance of sheep for wool production (Jacobsen 1969; 1973; Payne 1985). The adoption of larger scale animal husbandry practices may have altered the occupation patterns of these early farmers; traces of Middle Neolithic activity were found within two caves in the locality of Franchthi, which have been interpreted as evidence of transhumance (Jameson *et al.* 1994). Modern examples of transhumance take flocks to higher elevations to escape the scorching heat of the coastal plains and valleys, thereby ensuring that the flocks receive lush, nutritious grass; Halstead (1996) suggests that the Neolithic farmers periodically adopted a similar pattern, using these caves as sheep and goat folds as the herders exploited different pastures.

The settlement patterns within the Argolid are further suggested to have expanded very slightly during this period, Jameson *et al.* (1994) suggest that this does not necessarily reflect an increase in population, but rather an expansion in resource and landscape exploitation; the increased number of sites representing satellite herding camps or similar seasonally used bases. This would indicate that certain groups within the population were spending increased periods of time as animal husbandry practices became increasingly complex. The degree of contact with the animals may have negated infection rates by deflecting the vectors away from the humans; equally time spent at higher elevations would limit the risk of infection, as while some vectors can transmit at higher altitudes, successful transmission is extremely reliant on higher temperatures. Transmission is rarely as effective as along the coastal zones, where a greater percentage of *Anopheline* vectors predominate (Lividas *et al.* 1941; Becker 2003). Modern malaria studies from Greece and Africa indicate that pastoral communities and nomadic herders generally suffer higher parasite burdens when herding and grazing livestock within stream incised valleys (Barber *et al.* 1936; Anosike *et al.* 2004).

The Middle Neolithic farmers are therefore suggested to have been exposed to an increasingly high malariogenic capacity, which would have been augmented by the high humidity levels and temperatures of the first few centuries of the period. The increasingly arid climate, with low precipitation levels (Rohling *et al.* 2002; Geraga *et al.* 2005) may, however, have suppressed this capacity. Taxa such as *Ephedra* and *Artemisia* from the Kiladha Bay pollen cores, dated to c. 5765 and 5536 cal. BC (7714-7485 cal. BP), may reflect a transition to a drier climate and a more open environment. These hot, dry taxa, combined with the low frequencies of deciduous tree species, may reflect decreasing precipitation levels (Bottema 1990). It should, however, be noted that firstly, this alteration in taxa may have been influenced by anthropogenic activity and secondly, that the decline in humidity levels was entirely relative to the high levels of the HHP. The presence of *Tilia* and *Pistacia* trees

would indicate continuing moisture availability, suggesting that precipitation levels remained greater than those of the modern Aegean (Rossignol-Strick 1999; Rohling *et al.* 2002; Geraga 2005).

Water availability may have varied across the region, as evidence for an augmented deposition rate of calcareous deposits in Franchthi Cave dating to 5610 cal. BC (7559 cal. BP) have been interpreted as evidence of an "unusually wet period", suggesting increased rainfall or water availability (Vitelli et al. 1999:11). This may reflect the karstic system of the cave rather than elevated precipitation levels for the whole region; however it is suggested that a high water flow through the cave would indicate that the karstic streams along the coastal zone were equally as active. Modern empirical evidence for vector behaviour would suggest that local of water sources such as these, lying within an otherwise arid environment, would result in intense foci of vector populations across the littoral zone and in proximity to the Paralia (Bruce-Chwatt 1980; Bouma *et al.* 1996; Lounibos 2007). Risk of infection is therefore likely to have remained high in the locality despite the increasing aridity. It is also suggested that the coastal positioning of the site may have afforded the *Anopheline* vectors some protection against falling humidity levels; as such areas are far more humid than inland areas (Jameson *et al.* 1994).

It is concluded that the environment of the Franchthi headland was highly conducive to the malarial vectors throughout the Middle Neolithic period; the open, steppe-like environments as indicated by the pollen cores from Kiladha Bay would undoubtedly have been more conducive to the 'tropical' *Anopheline* than suggested by previous studies (Bruce-Chwatt *et al.* 1980; de Zulueta 1994). The variety of water bodies in the region, most likely limited in distribution, would suggest a high capacity for localised but high vector densities. Most significant to malaria studies is the evidence for expanding anthropogenic activities. Land

clearance, more intensive animal husbandry, perennial occupation patterns and a greater exploitation of the resource bases within this coastal region would suggest a significant malariogenic capacity and a high degree of anthropogenic exposure to the potentially malarious areas.

Discussion

Angels' (1969a; 1986) hypothesis of a high malariogenic capacity during the Mesolithic to Early Neolithic (subsequently re-dated to the Middle Neolithic) is therefore broadly supported by this reconstruction; despite numerous climatic oscillations, the climate and the ecological diversity of the area created a highly viable environment for the *Anopheles* vectors and the various malaria *Plasmodiae*. As noted in chapter three, the climatic capacity for malaria during the Mesolithic and Neolithic was particularly high; the elevated temperatures, highly augmented precipitation levels and muted seasonality would provide highly suitable conditions for perennial transmission, promoting rapid vector development and sporogonic cycles, while reproduction rates, biting rates and life span of the vector would all have been positively affected.

The Mesolithic environment appears highly viable for many vector species. The presence of open land, indicated in the faunal and floral assemblage from Franchthi Cave, contradicts Bruce-Chwatt (et al. 1980) and de Zulueta's (1994) hypothesis that the 'tropical' vectors, *A. superpictus* and *A. sacharovi,* would have been entirely excluded from the Aegean due to dense forestation (see chapter one). The evidence would instead suggest a landscape mosaic (Payne 1975; Hansen 1991; Jameson et al. 1994), composed of open parkland, maquis, and areas of grassland and coastal meadows, which would readily support small foci of these 'foreign' vectors along the Franchthi headland. It is clear that the distribution of these tropical vectors would not have been as expansive as the modern, due to the lack of anthropogenic

influence on the landscape; the wooded nature of the environment is therefore likely to have limited the vectors to predominantly coastal habitats. The malariogenic capacity for local vectors, which are more tolerant of woodland and shaded water bodies, is suggested to have been far higher; these *Anopheline*, several of which can transmit *P. falciparum* and all of which can transmit *P. vivax* and *P. malariae*, are suggested to have been primary vectors. It is therefore concluded that the climatic and environmental conditions of the Mesolithic period at Franchthi Cave would theoretically have been sufficiently conducive to support the introduction of *P. falciparum* and the *Anopheline* vectors that carry the strain, as well as *P. vivax* and *P. malariae*. The climatic tolerances of these latter strains are furthermore better suited to the cooler conditions of the Younger Dryas, suggesting that these strains may have predated the Mesolithic occupation of Franchthi Cave and may, therefore, have been well established during this period.

Although the malariogenic capacity, and human vulnerability to that capacity, is suggested to have been considerable during the Mesolithic, the possibility of endemic malaria is not suggested to have been significant until the Neolithic. While hunting and gathering may have exposed the Mesolithic populations to vector habitats, the gradual introduction of a settled farming economy at Franchthi Cave, including the domestication of animals, land clearance, crop cultivation and introduction of permanent dwellings, would have created new habitats for the *Anopheline* vectors in close proximity to the human occupants. These new anthropogenically created niches would have been highly favourable to the vectors, increasing lifespans, biting behaviour and abundance, thereby augmenting the risk of infection. In effect, the developments of the Initial to Early Neolithic caused vectors to adapt for the first time to anthropogenic micro-environments and microclimates, irrevocably altering vector behaviour and, as a consequence, changing potential malaria patterns.

The advent of larger scale land clearance would furthermore have altered the prevalence of vector habitats and therefore the frequencies of the sub-species; *A. plumbeus* is suggested to have been particularly prevalent during the Mesolithic to the Early Neolithic due to the suggested tree cover of the environment surrounding Franchthi Cave. The indications of an open steppic landscape during the Middle Neolithic period would suggest a reduction in the density of this vector in favour of open land and aridity tolerant vectors, such as *A. sacharovi* and *A. superpictus.* An ecological shift of this nature could result in a dramatic increase in abundance of such primary vectors, which is a crucial factor in successful transmission patterns (Bruce-Chwatt 1980; Yasuoka *et al.* 2007). The farming populations of Franchthi Cave are therefore suggested to have been increasingly vulnerable to malaria infection.

It is not suggested that malaria infection would have been ubiquitous or continuously perennial throughout these periods; the deterioration in winter temperatures and humidity levels after c. 6850/6650 cal. BC (8800/8600 cal. BP)[89], and again during the latter half of the Middle Neolithic period, would have limited the malariogenic capacity of the environment (see chapter three). It is proposed however, that the local environment and developing anthropogenic activities described above would have undoubtedly augmented the possibility of a heavy disease burden, potentially promoting a more intense transmission pattern as the warmer months would coincide with increased anthropogenic activity and, by consequence, greater exposure to viable vector habitats. The malariogenic capacity of the region of Franchthi Cave is therefore suggested to have been high; the climate and environment were undoubtedly viable for the successful transmission of all three strains of malaria.

[89] 7986±17 ^{14}C yr BP - 7840±15 ^{14}C yr BP (Reimer et al. 2004)

Chapter Five:

Environment and Malaria: The Early Neolithic Site of Nea Nikomedeia, Northern Greece

"Malaria is notoriously [...] the scourge of these lands"

Great Britain Admiralty (1916: 65)

Nea Nikomedeia, located on the plain of Veria in northern Greece, is situated in a region which was renowned as a malarial centre during the early twentieth century; a reputation which indicates an exceptional malariogenic capacity, given that Greece itself was considered the most malarious country in Europe (Balfour 1935; Lividas *et al.* 1941). Extensive studies into the disease were undertaken in Macedonia between the First World War and the early 1930s (Willoughby *et al.* 1918; Barber *et al.* 1936; Lividas *et al.* 1941); the extreme and well-documented prevalence of malaria during these periods provides an unparalleled insight into the relationship between the local climate, environment and malarial vectors. These malaria records, specifically those of the 1930s, may therefore serve as a modern analogue for the relationship between environment and malaria in the past.

Modern malarial studies

The high malariogenic capacity of the plain of Veria during the twentieth century was partly due to the varied topography of the plain; this provided a rich diversity of ecological niches, permitting multiple *Anopheles* vectors to co-exist, without the limiting factor of intra-species competition (Willoughby 1919; Balfour 1935; Barber *et al.* 1936; Horsfall 1955). The landscape combines multiple reliefs; as high altitude mountain ranges, hill-land, alluvial plain and coastline lie side by side within a 50 km by 30 km area (figure 5.1) (Rodden 1964; Bintliff 1976). The plain lies to the north and northwest of the Thermaic Gulf and is ringed by rugged mountain ranges. The north is bordered by the Paikon and Boras Mountains, the

Olympos Mountains lie to the south and the Pieria Mountains to the southwest, all of which range between 1149 m and 2917 m. The site itself lies at the foothills of the Vermion Mountains which reach up to 2,052 m in height (Sivignon 1983). The settlement of Nea Nikomedeia therefore lies within a basin, heavily sheltered from the south to the north by the rugged topography, which, combined with the strong maritime influences, creates a surprisingly mild microclimate. Winters are particularly mild in comparison with other regions of northern Greece (Sivignion 1983).

The wide variety of hydrological systems along the plain were particularly significant with regards to the malariogenic capacity during the twentieth century; the region forms the largest deltaic complex in Greece, measuring c. 2000 km^2, with multiple rivers intersecting the plain of Veria (figure 5.1). The largest of these, the Aliakmon and the Axios, lie to the south and to the east of the site of Nea Nikomedeia respectively, a smaller river, the Moglenitsa lies to the north and the Gallikos River flows to the west of Thessaloniki. The Loudhias River is a more recent creation which did not feature on the Neolithic landscape and Lake Giannitsa, lying to the north of Nea Nikomedeia, is no longer extant due to drainage programs during the 1930s (Bottema 1974; Fouache *et al.* 2008).

During the early twentieth century the plain was largely deforested, which strongly favoured the primary, sun-loving vectors of the region. The rivers were, however, lined with trees and overhanging vegetation, which created eddies and protective pools against the strong currents. These provided habitats for larvae which favour still or slow running water courses, while allowing sufficient sunlight to support larvae that favour warmer waters; studies from the First World War note that the most efficacious vectors of the area bred in and around these rivers (Willoughby *et al.* 1918). Heavy water logging of the soils surrounding the river

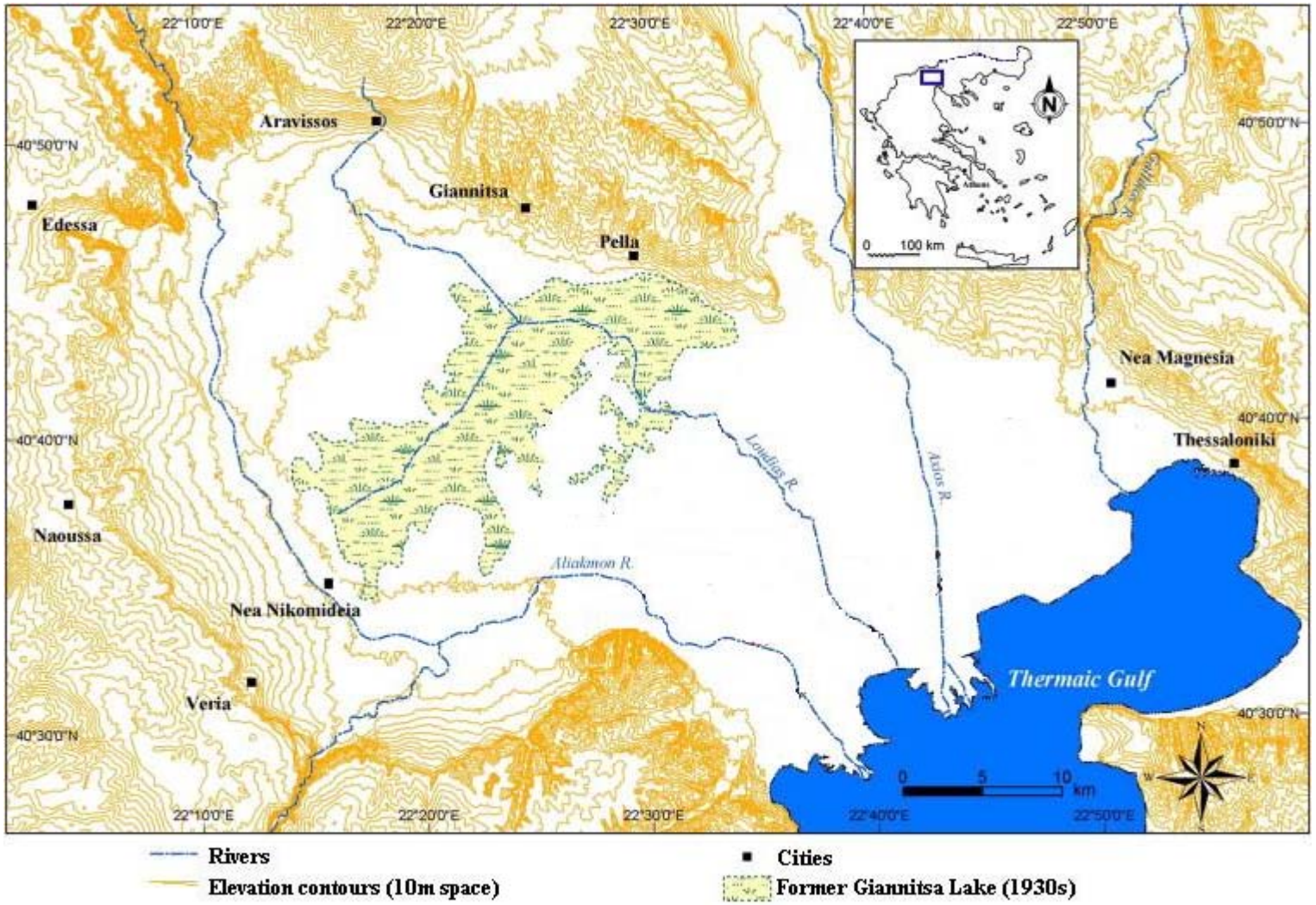


Fig. 5.1: Map of the modern configuration of the plain of Veria (*After* Ghilardi *et al*. 2010; fig. 1: pg. 179). Modified by author.

banks provided further breeding grounds and was exacerbated by fairly regular and extensive flooding; despite the construction of dams, the rivers frequently burst their banks and submerged the flatter areas of the plain and whole villages are reported to have been swept away by dramatic floods caused by the Aliakmon and Axios (Bottema 1974).

The Admiralty handbook (1916) indicates that malaria was "peculiarly prevalent […] the most dangerous places [were], of course, the neighbourhoods of marshes or lagoons" (Great Britain Admiralty 1916: 65). Marshland was extremely extensive across the plain, measuring 90 km^2; heavily waterlogged soils lay alongside the banks, along the coastline and surrounded the mouths of the rivers, especially the Axios and Aliakmon. The entire central plain was avoided by local inhabitants due to the threat of infection and, although grazing of livestock was common, the land largely remained uncultivated (Lividas *et al.* 1941; Bottema 1974; Borza 1979; 1992). An extensive drainage and anti-flooding program was undertaken between 1925 and 1940 to increase the agricultural value of the area and to reduce the high malariogenic capacity for which the area was famed (Psimoulis *et al.* 2007; Sivignon 2007). The program was successful and drastically altered the natural landscape of the plain; however the prevalence of malaria remained considerable (Balfour 1936; Lividas *et al.* 1941). This would indicate that other water bodies, such as the coastal waters and rivers, must have contributed significantly to the malariogenic capacity of the plain.

The coastal waters and saline marshes are suggested to have been particularly dangerous, promoting high population densities of the saline tolerant and brackish breeders, *A. sacharovi*, *A. hyrcanus*, *A. atroparvus* and *A. algeriensis* (Great Britain Admiralty 1916; Willoughby *et al.* 1918). It is further interesting to note that the malariogenic capacity in the Veria Plain during the early twentieth century remained high even during periods of aridity; malaria remained "peculiarly prevalent in the plains, even in those which during the summer

…[were]… absolutely devoid of water" (Great Britain Admiralty 1916: 65).

The malariogenic capacity of the landscape therefore lay partly in the volume of the water, as the rivers, extensive marshland, lagoons and coastal marshes all lay within one small region. The different types of water were also particularly significant, as brackish, fresh, stagnant and flowing water bodies created an area of extraordinarily high malariogenic capacity, providing every conceivable style of breeding ground favoured by the malarial mosquitoes of the region. The landscape could therefore support multiple vectors, which undoubtedly contributed greatly to the high frequency of malaria during the early twentieth century; the overlapping life cycles of each vector gave rise to long transmission seasons, which were particularly conducive to high infection rates. Winter temperatures, although milder than those of other regions, limited this malariogenic capacity until early spring; however the high winter rainfall caused sharp increases in vector populations once temperatures increased, resulting in a marked endemic-epidemic cycle with a high mortality and morbidity rate (Balfour 1935; Barber *et al.* 1936).

Historically, the primary vectors of the area are *A. sacharovi*, *A. superpictus* and *A. maculipennis* (Balfour 1935). Some studies from the region have indicated that *A. superpictus* is a less effective carrier of *P. falciparum* than in other regions; despite a high sporozoite index, the sporozoites appeared to degenerate rapidly both in laboratory and natural conditions (Barber *et al.* 1932). In Macedonia, *A. superpictus* was also shown to have stronger zoophilic tendencies than anthropophilic and therefore, despite an extremely rapid larval development rate and faster digestive process, this vector did not *always* contribute to the *P. falciparum* burden as much as may be expected (Barber *et al.* 1932; Lividas *et al.* 1941). Other studies disagreed with this theory however, noting that the autumnal peak in *A. superpictus* populations could be considered accountable for prolonged transmission seasons and seasonal peaks in *P. falciparum* infections (Balfour 1936). This chapter will consider this

vector to be efficient, although possibly secondary to *A. sacharovi*.

Other vectors have had a stronghold in the north of Greece during modern history. *A. hyrcanus* has been noted as a particularly prevalent species; during the early twentieth century, this vector (then identified as *A. pseudopictus*) was considered to be associated with a heavy malaria burden (Willoughby *et al.* 1918). *A. algeriensis*, *A. marteri* and *A. claviger* have all been noted in Macedonia but none were considered to contribute to the malarial burden in any significant way, either due to marked exophagic behaviour, limited population densities, or an inability to successfully harbour the malaria *Plasmodiae* under laboratory conditions (Lividas *et al.* 1941). These vectors may, therefore, have contributed to malaria patterns but would not have supported the disease without the presence of one or several primary vectors. *A. plumbeus* was also once common in the Macedonian region but there is little information on its contribution to the disease burden (Peus 1954).

The modern history of the plain, the local climatic and environmental conditions and malarial transmission patterns, provide a highly useful frame of reference with which a prehistoric reconstruction can be compared. It is not suggested that the malaria patterns of the twentieth century accurately reflect those of prehistory, as the anthropogenic influences and socioeconomic factors of these periods differ considerably. The endemic-epidemic cycles in Greek Macedonia during the early twentieth century were strongly influenced by population movements, as army troops and refugee populations moved into Macedonia and northern Greece in 1915-1918 and again during the early 1930s (Kontogiorgi 2006). Equally, anthropogenic activities such as water management techniques, deforestation and large scale agriculture had significant impacts on *Anopheline* populations and, therefore, on infection rates (Lividas *et al.* 1941). However, some malariogenic determinants, such as the general topography, the position and climatic effects of the mountain ranges and the climatic and environmental effects on the local vectors, are not considered to have changed. These records

may therefore serve as an invaluable frame of reference.

Reconstruction of the environment and malariogenic capacity of Nea Nikomedeia

The Early Neolithic (*c. 6414- 5924 cal. BC/ 8363-7765 cal. BP*)

Angel's (1973) interpretation of the osteological data dating to the Early Neolithic (figure 5.2) from Nea Nikomedeia indicated an exceptional frequency of *Porotic hyperostosis* and, by inference of β-thalassemia, which led him to conclude that "some other source of anaemia" was contributing to create such a high incidence (1973: 105). He proposed, however, that *P. falciparum* was one of the primary causes of the condition and that the malariogenic capacity of environment must, as in modern history, have been extremely high (Angel 1973).

Reconstructions of the Veria Plain indicate that considerable environmental changes have occurred since the Early Neolithic. While the topography of the region has remained stable, bathymetric evidence and pollen cores indicate that the vegetation cover, hydrological systems of the plain and sea levels have changed significantly during the intervening millennia. The malariogenic capacity of the local environment would therefore have differed considerably from that of the modern. The 'toumba', or tell site, of Nea Nikomedeia occupies a low rise mound on dried lacustrine silts approximately 10.5 km north-east of the modern town of Verroia (Pyke 1996). Based on sedimentological data, Bintliff (1976) suggests that the immediate surroundings of the site during the Early Neolithic were well-drained, with none of the ground water problems that characterised the waterlogged landscape of more recent history.

Chronological period cal. BC in northern Greece (Andreou *et al. 1996*)	Lab Sample	^{14}C Age	Cal. BP σ 2	Cal. BC	Median cal. BC	Ref.
Early Neolithic 6700/6500-5800/5600	Q-655	8180±150	9481-8658	7532-6709	7188	(1)
	GX-679	7780±270	9397-8048	7448-6099	6715	(1)
	P-1202	7557±91	8540-8186	6591-6237	6414	(1)
	OxA-1606	7400±100	8387-8018	6438-6069	6274	(1,2)
	OxA-1605	7400±90	8379-8028	6430-6079	6277	(2)
	OxA-4282	7400±90	8379-8028	6430-6079	6277	(1,2)
	OxA-3874	7370±80	8353-8018	6404-6069	6242	(1,2)
	P-1203A	7281±74	8302-7956	6353-6007	6149	(1,2)
	OxA-3873	7300±80	8313-7968	6364-6019	6163	(1,2)
	OxA-3876	7370±90	8366-8014	6417-6065	6242	(2)
	OxA-1604	7340±90	8348-7981	6399-6032	6206	(1,2)
	OxA-3875	7280±90	8315-7950	6366-6001	6152	(1,2)
	OxA-4283	7260±90	8311-7934	6362-5985	6137	(1,2)
	OxA-4281	7100±90	8157-7721	6208-5772	5972	(1,2)
	OxA-1603	7050±80	8007-7703	6058-5754	5926	(1,2)
	OxA-4280	6920±120	7970-7572	6021-5623	5924	(1,2)

Fig. 5.2. Early Neolithic occupation of Nea Nikomedeia, Plain of Veria, Northern Greece. **1)** Pyke *et al.* 1996, **2**) Perlés 2001, **3)** Reingruber *et al.* 2005. Calibrated with OxCal 4.1. Dates Q-655 and GX-679 are considered aberrant due to an uncertain provenance and, in the case of GX-679, a large standard deviation. These samples are therefore commonly rejected (Bintliff 1976; Perlès 2001; Weninger et al. 2006).

Breeding grounds are not, therefore, considered to have lain in the immediate vicinity of the site; however, the settlement of Nea Nikomedeia lay in far greater proximity to the coastline than it does today, as much of the plain was then occupied by a large, shallow marine inlet from the Thermaic Gulf (figure 5.3) (Bottema 1974; Bintliff 1976; Fouache *et al.* 2008). A radiocarbon date of 7260 ^{14}C yr. BP (6208-6065 cal. BC/8157-8014 cal. BP)[90], taken from early estuarine sediments, suggests that this marine transgression was broadly contemporary with the Early Neolithic occupation of Nea Nikomedeia (Bottema 1974; Bintliff 1976). Radiocarbon dates from six cores taken across the plain indicate that a fast deltaic progradation process began in the Early Bronze Age, where alluvial sediments deposited by the various rivers that transect the plain gradually in-filled the inlet (Fouache *et al.* 2008).

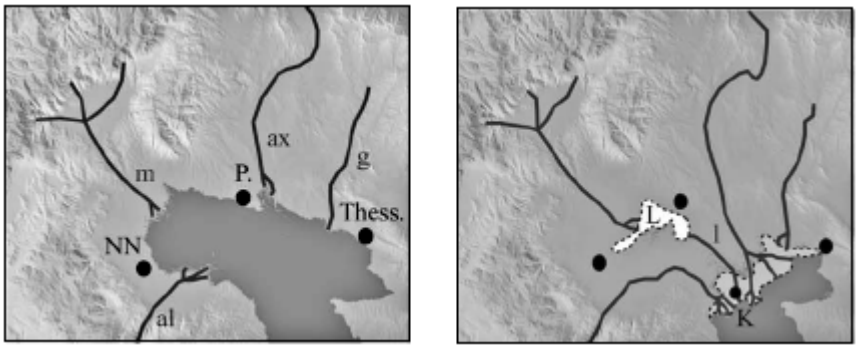


Fig. 5.3. Marine occupation of the plain during a) the Neolithic to c. 3000 BC and b) by 1904

Key: **al**- Aliakmon River; **m**- Moglenitsa River; **ax**- Axios River; **g**- Gallikos River. **NN**- Nea Nikomedeia, **P**- Pella and **Thess**- Thessaloniki. **L**- Lake Giannitsa, white background indicating Limnic occupation; **l**- Loudias River; (**K**-Klidi Roman Bridge) (*After* Fouache *et al.* 2008: fig. 10: pg. 1170).

[90] Calibrated with OxCal 4.1

Whether the shores of the inlet provided viable habitats for *Anopheline* vectors is debatable. Abundant mollusc fragments within a sediment core situated to the northeast of Nea Nikomedeia indicate strong energy levels of a beach environment, which would indicate that the waters of the inlet were not suitable for oviposition (Fouache *et al.* 2008). The core, dating to the Bronze Age period (4083-3947 cal. BC/ 6033-5897 cal. BP)[91], may not be pertinent to the period in question; however the data must be considered when reconstructing the malariogenic capacity of the Neolithic (Fouache *et al.* 2008).

If beach environments did exist during the Early Neolithic, they were mixed with areas of less active coastline. Although detailed bathymetric evidence for this period is lacking, an interpretation of pollen data from Lake Giannitsa, lying at 8 km north-east of Nea Nikomedeia (figure 5.4), indicate areas of low-energy coastline (Bottema 1974). Two radiocarbon dates place this pollen record at 6141-5538 cal. BC[92]; based on sedimentation rates, comparisons with adjacent cores, archaeobotanical and archaeological evidence, Bottema (1974) suggests that the sedimentation of the core began in c. 8500 BP (c. 6550 BC). The pollen record is therefore considered coeval with the initial settlement of Nea Nikomedeia and the data therefore may reflect the contemporary environment.

Halophytic plants, such as *Salicornia* (samphire grass) and other *Chenopodiaceae* species, are relatively common in the pollen data from Lake Giannitsa (Bottema 1974: 141; fig. 34). These species grow within saline soils and predominantly within saltmarshes, environments which only occur along low-energy coastlines. Saltmarshes, or coastal marshes, are protected

[91] 5730±35 ^{14}C yr BP (Fouache *et al.* 2006).

[92]

^{14}C yr BP	**Cal. BP σ2**	**Median cal. BC**
7270±70	8285-7953	6141
6590±110	7662-7293	5538

Bottema (1974) notes however that these radiocarbon dates must be cautiously accepted due to a small sample size and poor preservation. Calibrated with OxCal 4.1.

from heavy wave actions by intertidal flats and barriers; these ecosystems are therefore highly favourable to the saline tolerant mosquitoes, such as *A. sacharovi, A. hyrcanus, A. algeriensis* and *A. atroparvus* (Allen *et al.* 1992; Becker 2003). Bottema (1974) notes that it is difficult to differentiate local and regional pollen data from the Giannitsa core due to the wide catchment area of the lake and that the extent of these marshes cannot be ascertained from just one pollen diagram; however it is suggested that the saline tolerant plants pertain to the coastal inlet. This evidence may therefore indicate that different environments developed along the coastline of the inlet and *Anopheline* population densities may have varied across the coastal zone.

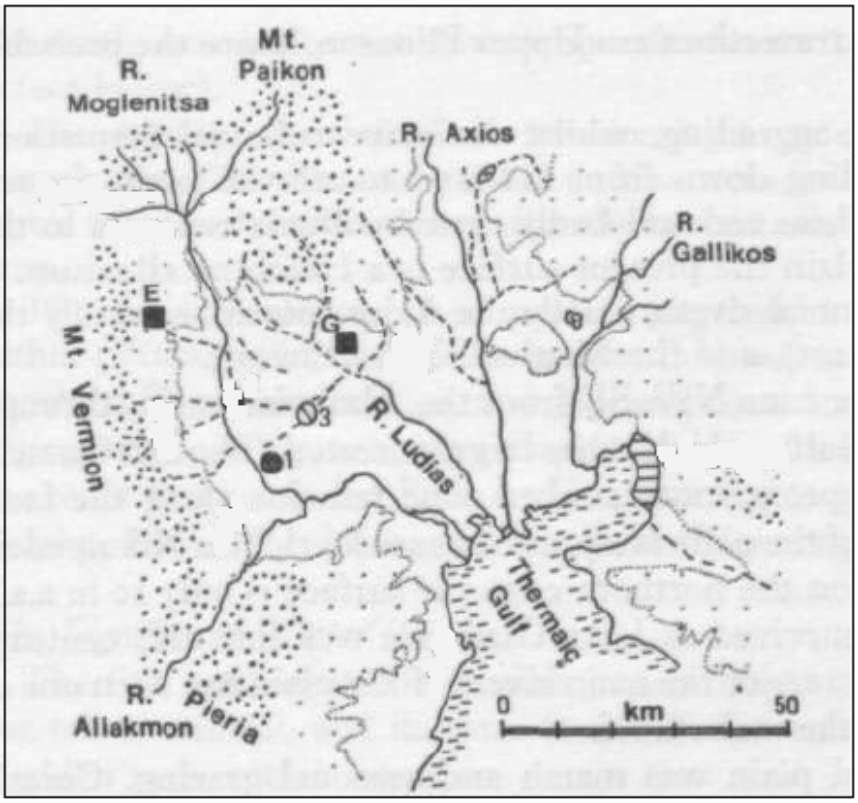


Fig. 5.4. Map showing modern configuration of the plain of Veria and the location of the pollen cores **Key: 1:** Nea Nikomedeia. **G:** Giannitsa pollen core. **E**: Edessa pollen core (*After* Bintliff 1974: fig. 1: pg. 243). Modified by author.

Oxygen isotope studies on *Cerastoderma edule* (L., 1758) (cockle shells) from the faunal assemblage at Nea Nikomedeia indicate that the water quality of the inlet fluctuated. Saline conditions predominated during the summer and became diluted with fresh water during the winter months, indicating an open estuarine environment (Shackleton 1970). Based on modern studies of the high freshwater inputs into the Thermaic coastline, which are predominantly deposited from the Axios, Aliakmon and Gallikos rivers (Poulos *et al.* 2000) and palaeoclimatic evidence for excessively high precipitation levels during the Early Neolithic (Kotthoff *et al.* 2008a), it could be suggested that the influx of fresh water was considerable. The resulting variable water quality would result in fluctuating *Anopheles* densities; heavy rainfall or flooding events during the spring would have diluted the salinity of coastal marshes, increasing the viability of the habitat for brackish-water breeders, rather than just the saline-tolerant. The changes in water quality would be rapidly exploited by vectors, suggesting a potential for abrupt increases in malariogenic capacity (Lividas *et al.* 1941; Lindsay *et al.* 1996a).

The exact position of the coastline in relation to Nea Nikomedeia is extremely important with regards to the degree of exposure of the human population to these coastal marshes, but remains a subject of considerable debate. Shackleton (1970) argues that the source of the common cockle must have lain in close proximity to the site, as the nutritional value of this bivalve is not sufficient to warrant carrying them over long distances. Based on this and the use of wetland materials in the construction of the houses at Nea Nikomedeia, Rodden (1964) concluded that the site lay “on the edge of [an] inlet or marsh” (1964: 85), a supposition that is supported by Bottema’s (1974) reconstruction of the plain based on palynological data. This would indicate that Nea Nikomedeia lay in extreme proximity to malarious waters, indicating potentially high exposure to *Anopheline* vectors. Conversely, Bintliff’s (1976) geomorphological study indicates that the inlet was at least 5 to 6 km from the site, which

would suggest that the saline waters of the inlet posed a minimal risk to the settlement as the flight range of the *Anopheline* mosquito only extends up to 5 km (Lividas *et al.* 1941).

Fouache *et al*'s (2008) more recent geomorphological study concludes, however, that there is no biostratigraphic evidence to support either of these theories. The distance between the site and inlet therefore remains uncertain. It may be suggested, however, that the malariogenic capacity would have been considerable even if at a greater distance from the site, assuming that modern wind patterns are an analogue for those of the prehistoric (Swellengrebel 1929). The north-easterly summer Etesian winds and the continuous sea-breezes from the south-east would have undoubtedly served to propel vectors from the coastal waters and marshland towards and into the settlement. Lividas (*et al.* 1941) reports a similar scenario, where the occupants of Levadia in southern Greece during the 1930s feared winds blowing from the notoriously malarial Kopaïs Basin, as an invasion of virulent mosquitoes and consequently extremely elevated infection rates would follow. It is concluded therefore that the inlet and coastal saltmarshes created a considerable malariogenic capacity across the plain and posed a potential threat to the population of Nea Nikomedeia.

Sedimentological analysis of alluvial deposits, pollen data and faunal remains indicate that the major rivers of the modern plain were active during the Early Neolithic (Bottema 1974; Bintliff 1976; Fouache *et al.* 2008). These rivers have minimally altered in their courses over the millennia. Sediment analysis from the Giannitsa core indicate that by 6363-5990 cal. BC (8312-7939 cal. BP)[93] alluvial deposition from one of the local rivers, either the Aliakmon or the Moglenitsa, had altered, as sediments were deposited closer to the coring site than before (Bottema 1974). It appears that the river courses have not substantially altered, however, as remains of the thick-shelled river mussel (*Unio crassus*) in the faunal assemblage at Nea

[93] 7270±90 ^{14}C yr. BP (Bottema 1974) calibrated to 2σ with OxCal 4.1.

Nikomedeia (Clench 1962 in Rodden 1962), suggest that fresh water rivers remained in reasonable proximity to the settlement during the occupational period. Like cockles, the nutritional value of the mussel is small and is unlikely to have been gathered from great distances (Clench 1962 in Rodden 1962).

Pollen frequencies from the Giannitsa core indicate a high percentage of riparian taxa such as *Salix* (L.) (willow), which is likely to have overhung river banks (Bottema 1974). The precipitation levels of the Neolithic, suggested to have been higher than those of the modern (see chapter three) (Kotthoff *et al.* 2008a), would indicate a potential for swift river currents. The volume of surrounding overhanging vegetation, such as *Salix, Fraxinus excelsior, Vitis* and *Alnus* (Mill.) (alder) (Bottema 1974) would therefore be integral to the survival of the eggs and larvae, providing secure breeding grounds for the *Anopheline* vectors.

Interpretations of the pollen cores from Giannitsa furthermore suggest that the water table of the plain was high and, combined with evidence for marshland taxa such as *Polygonum aviculare* (L.) (knotgrass) and Dryopteris spp. (Adans.) (wood ferns), Bottema (1974) concludes that the plain was "transected by small, fresh water streams which formed small ponds or fresh water marshes [...creating...] a mosaic of fresh water and saline habitats" (1974: 148). The variety of fresh and brackish water in rivers, pools, marshland and coastal waters would therefore provide an abundance of breeding grounds and, as the malarial studies from the early twentieth century indicate, this would allow both primary and secondary vectors to breed side by side without the need for intra-species competition (Willoughby *et al.* 1918; Balfour 1935; Barber *et al.* 1936).

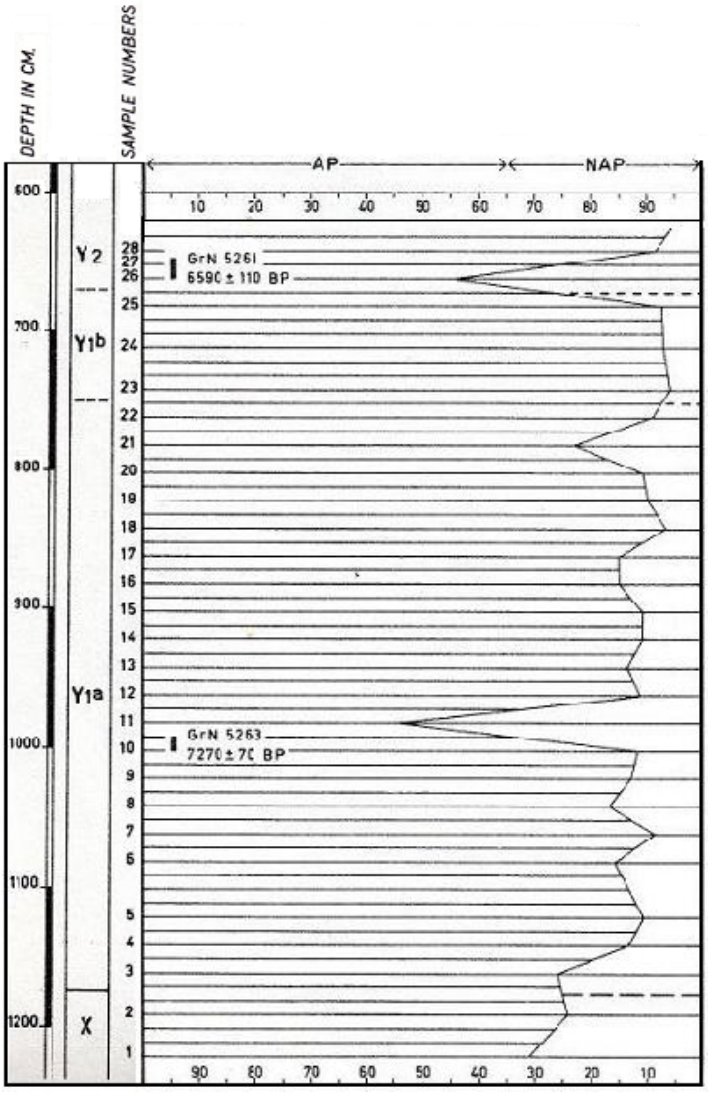
The decline in humidity and the decreased winter temperatures of 6250 cal. BC (8200 cal.

BP)[94] are suggested to have reduced the malariogenic capacity. The c. 2 °C drop in winter temperatures, noted in chapter three, would have shortened the potential transmission seasons considerably, limiting the malariogenic capacity to the spring, summer and autumn months. The decrease in precipitation in the northern regions was, however, minimal and the water availability and river flow would not have been affected significantly. Kotthoff (*et al.* 2008a,b) suggested that winter precipitation levels remained highly elevated in comparison with the modern, averaging at c. 300 mm, suggesting that the volume of breeding grounds would have remained high. It is therefore concluded that the area surrounding Nea Nikomedeia would have retained a significant malariogenic capacity during this climatic deterioration, although transmission patterns are tentatively projected to have been highly unstable. The low winter temperatures would impose a significant hiatus on infection while the high winter precipitation would provide high volumes of surface water; the increase in temperatures during spring would therefore be suggested to have resulted in rapid increases in vector density, and a concomitant rise in infection rates. Modern empirical evidence would suggest that such conditions could result in virulent outbreaks of malaria (Bouma *et al.* 1996; Lindsay *et al.* 1996a).

The forestation of the plain is suggested to have restricted the malariogenic capacity resulting from the high volume of water across the plain. Pollen data from Lake Giannitsa and Edessa (figure 5.4) indicate that the plain of Veria was far more extensively forested than the modern landscape (Bottema 1974), which would, as suggested by Bruce-Chwatt (*et al.* 1980) and de Zulueta (1994), have limited the capacity of the environment for the sun-loving primary vectors. Evergreens are suggested to have predominated at higher altitudes, thick deciduous forests composed of *Quercus*, C*orylus*, *Pistachia* and *Tilia* covered the lowlands, while the river valleys and marshland were bordered by *Salix*, *Vitis* and *Alnus* (Bottema 1974). The tree

[94] Commonly dated to 7400/7500 ^{14}C yr BP (Alley *et al.* 1997; Weninger *et al* 2006).

cover was not entirely continuous however; even in the absence of widespread deforestation by human agency, the landscapes of prehistory are suggested to have been a patchwork of different vegetation types due to, for example, differing soils, altitudes, aspect and water availability (Rackham 2001). Pollen data from Lake Giannitsa supports this contention, indicating the existence of open areas of land (figure 5.5).



6590±110 ^{14}C yr BP (7662-7293 cal. BP/ 5713-5344 cal. BC)

7270±70 ^{14}C yr BP (8312-7939 cal. BP/ 6363-5990 cal. BC)

c. 8500 BP/ 6550 BC (Based on sedimentation rates)

Fig. 5.5. Pollen diagram from Lake Giannitsa showing frequencies of arboreal pollen (AP) and non-arboreal (NAP) pollen during the Neolithic occupation of Nea Nikomedeia. Two radiocarbon dates indicate a sedimentation rate of c. 1 mm per year (*After* Bottema 1974: figure 34). Modified by author.

Bottema (1974) suggests that the tree cover diminished towards the coast, opening onto saline meadows characterised by saline taxa such as *Tamarix* spp. (tamarisk), to the east and north east of the site and eventually to coastal marshes (Bottema 1974). Shrubland taxa was common and was most likely to have been distributed along the steep slopes of the mountains and along the low foothills; Bottema (1974) suggests that taxa such as *Juniperus* (Juniper) covered the lower altitudes of the Vermion Mountains, lying in close proximity to the site. Such vegetation is known to be capable of supporting *A. sacharovi* habitats, given adequate water sources (Kuhn 2002). Many of the vectors are, furthermore, capable of surviving and transmitting malaria at higher altitudes (see chapter two) which would have allowed the species to survive amongst the areas of shrubland along the steep mountain sides (Becker 2003).

The forested regions and marsh forest, surrounding highly waterlogged soils to the east/north-east of Nea Nikomedeia, would have strongly favoured the woodland vector *A. plumbeus* and other vectors which favour shaded water bodies, while the open saline meadows which lay along the coastal zone would have provided prime breeding grounds for *A. algeriensis, A. hyrcanus, A. atroparvus* and, most significantly *A. sacharovi*, which is tolerant of surprisingly high salinity levels (Bates 1970; Jetten *et al.* 1994; Iasiukevich 1997).

Further evidence of open land comes from the relatively high values of *Cerealia* in pollen cores from both Edessa and Giannitsa; Bottema (1974) interpreted these as representing natural clearings rather than agricultural, as there is no evidence of cultivar weeds, such as *Rumex* or *Plantago lanceolata* (Bottema 1974). One further, although meagre, indicator of open land comes from the discovery of one tortoise amongst the faunal remains, which indicates the presence of grassland (Higgs 1962). The extent of agricultural or deforested land is therefore unclear; some areas must, however, have been cleared by the farmers in order

that cultivation could take place and it would appear logical that open areas would be created alongside the rivers and in reasonable proximity to the site; these areas may have been frequented by the primary, sun-loving vectors which are known to strongly favour agricultural land (Becker 2003).

The landscape would therefore have been more hospitable to *A. sacharovi* and *A. superpictus* than suggested (Bruce-Chwatt *et al.* 1980); however, the proportion of open land in comparison to the prevalence of woodland would suggest that these *Anopheline* vectors would have been limited in distribution and concentrated in small foci across the plain. The landscape of the Neolithic could not have supported a mosquito density such as that reported during the 1930s, when the plain of Veria was hugely deforested and human population densities were high (Barber *et al.* 1936; Lividas *et al.* 1941). The areas of open land during the Neolithic do appear to have been sufficient, however, to suggest that the vectors would have been limited rather than excluded; the areas of shrub which covered the foothills and steep slopes surrounding the plain, the open marshes, saline meadows and treeless coastal zone would appear to have been sufficiently clear and sufficiently substantial to accommodate small populations of the suggested local vectors.

The suggested limited distribution of these primary vectors would shed doubt on the contention that malaria was highly endemic during the Early Neolithic occupation of Nea Nikomedeia; however, that malaria could have been transmitted appears plausible. The historical secondary vectors, *A. maculipennis, A. algeriensis, A. hyrcanus* and *A. claviger,* all of which favour shaded habitats, could have survived in greater population densities within this forested landscape. The virulent and anthropophilic *A. plumbeus* is suggested to have been highly prevalent. The extensive woodland would have been extremely conducive for this sylvan mosquito; breeding grounds would have been plentiful as the vector favours water filled holes in *Tilia* and particularly in *Quercus* (Aitkin 1953; Becker 2003), both of which

appear to have been abundant in the deciduous forests along the plain (Bottema 1974). Whether this vector could have contributed to a heavy malaria burden is questionable; the vector is rarely referred to in modern malarial literature from Greece due to its increasing rarity. However, studies from other countries in the Palaearctic region indicate not only the vectors efficiency as a carrier for all three *Plasmodiae* (Krüger *et al.* 2001; Eling *et al.* 2003) but also that it can contribute to the malaria burden when sufficiently abundant (Blacklock *et al.* 1920a; Gutsevich *et al.* 1974; Becker 2003; van Bortel *et al.* 2009). The vector will breed within urban settings, will feed in indoor contexts and is voraciously anthropophilic; in high densities, it is conceivable that this vector may have contributed to a heavy disease burden (Blacklock *et al.* 1920b; Becker 2003). It is, therefore, suggested that the malariogenic capacity of the plain was high despite the forest cover; *A. sacharovi* and *A. superpictus* would have been limited to small population densities but could still have survived on this coastal plain while the 'native' vectors could potentially have thrived under such conditions. Endemic transmission would therefore appear plausible if the occupants of Nea Nikomedeia were sufficiently exposed to these vectors.

Landscape exploitation and economic changes associated with the introduction of farming would have undoubtedly increased the vulnerability of human populations to infection. The farming revolution would have irrevocably altered disease patterns, as populations became permanently sedentary, local ecosystems were altered and animals became domesticated livestock; all of which would have altered the behaviour of local vectors (Yasuoka *et al.* 2007). Hansen (1991) suggests that foraging was still practiced although it appears to have been a distinctly secondary resource to crops, representing very little of the total floral assemblage. The foraged species identified would, however, indicate that the Neolithic populations spent time within highly malariogenic areas, as *Ficus* (L.) (fig), pear, grape, acorn, pistachio, almond and wild vetch would have been sourced from the river banks and

foothills, in proximity to both sun-loving vectors habitats and woodland habitats (Hansen 1991). The cultivation of crops is likely to have increased vulnerability to infection. The settlement is considered to have been occupied the year round (Wardle *pers. comm.* 2008) and this suggests that the full cultivation cycle was completed. Archaeobotanical evidence from Nea Nikomedeia indicate that *Triticum dicoccum* (Schübl.) (emmer wheat) *and T. monococcum* (L.) (einkorn wheat) were cultivated along with *Hordeum vulgare* (L.) (six- row barley), *Lens culinaris* (Medik.) (lentils) and *Piscum sativum* (L.) (pea); the harvesting cycle of which varies between spring (*Hordeum* and *Triticum*) and autumn (legumes and pulses). The time consuming process of sowing and harvesting would, therefore, have coincided with the peak in the vector populations (Balfour 1935; 1936; Hansen 1991).

The exact location of the cultivated soils at Nea Nikomedeia is not certain; despite ample evidence of crop cultivation from floral remains, the pollen assemblages from Giannitsa and Edessa do not record any significant deforestation dating to this period, indicating that the cultivated areas were limited in size (Bottema 1974). Estimates as to the population size of Nea Nikomedeia, varying between a conservative estimate of 120-240 inhabitants (Halstead 1981a) and a more generous estimate of 500-700 inhabitants (Pyke 1996) indicate that the area of cultivated land would not need to have been excessively large; it must, however, have been of a reasonable size, as surplus goods are known to have been acquired and stored on site (Pyke 1996). It is logical to suggest that the cultivation of cereals would have taken place on the well-drained lacustrine soils in close vicinity to the site; many of the early Neolithic sites tended to concentrate on and around the fertile alluvial soils due to the good water retention, irrigation potential and the considerable lightness of the soil. This permits tillage to take place by human hand, where the early farmers used digging sticks; cultivation of light soils would be an important factor given the absence of draft animals and, by inference, the potential for deep ploughing in Greece during this early period (Demoule *et al.* 1993).

The range of crops noted within the floral assemblage require well-drained soils with no excess water (van Zeist and Bottema 1971; Oplinger *et al.* 1989; McKay *et al.* 2003; Wainwright *et al.* 2004); the dry lacustrine soils therefore appear to have been a logical choice for the Neolithic farmers, having the obvious added advantage of easy irrigation from the river (van Zeist and Bottema 1971). The malariogenic capacity of these areas would have been considerable due, firstly, to the proximity to the water bodies and secondly, due to suggested pH of the soils in which the crops were sown (see chapter four). The type of crops listed favour similar pH levels as local vectors; therefore, assuming these crops were planted in suitable, productive soils with apposite pH levels, the cultivated soils and water bodies within the area would have been highly suitable for the local vector to oviposit (Oplinger et al. 1989; Patz et al. 2000; Kampen et al. 2004). Labouring on these alluvial soils would, therefore have increased the risk of infection from the sun-loving vectors.

The economic behaviour with regards to animals would have greatly influenced malarial patterns. Hunting was still practiced: deer and brown hare were hunted from the uplands and wooded areas and birds and fish bones were common. The remains of one tortoise were recovered; however, the uniqueness of this find strongly suggests that it did not form part of the Neolithic diet (Higgs 1962). Shell-fish are not well represented in the assemblage except in the case of the common cockle (Shackleton 1970). The economy was strongly biased to domesticated animals, as these wild resources constituted a mere 10% of the total faunal assemblage, indicating that the inhabitants relied largely on domesticates and agricultural produce (Rodden 1963). Cattle, ovi-caprines and pigs were introduced; however an estimate as to the sizes of these herds is unfortunately not possible; water-sieving was not used during excavation and consequently a large body of evidence has been lost.

It is tentatively suggested, based on the few and highly fragmented faunal remains, that, much like at Franchthi cave, sheep and goats predominated, with pig and cattle in lesser, but

still significant quantities (Higgs 1962; Watson 1972). The ratio of juvenile animals within the faunal assemblage indicates a more intense use of these animals; the majority were killed before their fourth year, potentially indicating a meat-producing economy (Payne 1987 cited in Davis 1987). A heavy reliance on meat requires the animals to be extremely well fed and it may be suggested that much time would have been spent feeding, herding and grazing the livestock so that the meat would have a high fat content and a decent nutritional return. Pigs will happily live amongst woodland and those who watched the herds would therefore have been more exposed to *A. plumbeus* than any other vector. Cattle, however, require large quantities of well-watered grazing land and it is suggested that the saline meadows represent the only archaeologically visible area for these animals to graze. These marshy areas lying along the coastline and surrounding the rivers, provide excellent pastureland, and were still used as cattle grazing during the twentieth century (Bottema 1974); they would also represent prime breeding grounds for the saline tolerant vector, *A. sacharovi* and the marsh breeders, such as *A. superpictus, A. maculipennis* and the secondary vectors *A. algeriensis, A. atroparvus* and *A. melanoon*. The vegetation, or swamp forest, surrounding these areas would furthermore have supported *A. plumbeus.* This economic behaviour may well therefore have exposed the settlers to considerable risk of infection, as guarding the livestock would entail time spent close to high volumes of surface water during the warmest months of the year.

The ovi-caprine herds, on which it is suggested that the dietary emphasis was placed, would have put considerable pressure on the labouring forces, especially within a landscape where tree cover or arable land limits the areas of grazing land (Halstead 1996). Goats will graze shrubby mountain sides in great numbers with minimal supervision; areas which are suitable breeding grounds for vectors favouring open ground. Sheep are, however, more discerning, requiring good grassland and considerable supervision. In a mixed wooded landscape with minimal grassland, such as that reconstructed from the palaeoenvironmental evidence, a large

herd would have had to have been divided into small groups in order to take advantage of the available land. This requires a greater number of herders in order that the flocks may be protected and if grazing is sparse, sheep may be grazed in rota to maximise resources, with some out at night (Koster 1977 in Halstead 1996). This would increase the vulnerability of the farmers and herders to infection, as they would work in the only open areas of the landscape alongside the watercourses and in close proximity to the livestock; both zoophilic and anthropophilic vectors would be attracted to these groups, especially at dusk or dawn.

Transhumance is a possible solution to the mixed nature of the landscape; in modern times flocks grazed along the plain during the winter, as the winters were sufficiently mild and wet to allow grass to grow throughout the colder months. During the summer months, shepherds moved the flocks to higher pasture land in the mountainous areas (Sivignon 1983). Many of the primary and secondary vectors can transmit at higher altitudes; *A. plumbeus*, *A. maculipennis* and *A. claviger* can all thrive at 2000 m, while the primary vectors *A. sacharovi* and *A. superpictus* can successfully transmit at over 1000 m (Becker 2003). Nonetheless, infection rates are lower at these elevations, as vector population densities are limited.

Transhumance in Greece has been linked to lower infection rates; Barber (*et al.* 1936), upon examining the disease burden of the Vardar populations from the highly malarious plain of Crysoupolis in eastern Macedonia, noted no parasite index amongst the herders at all due to their seasonal economic behaviour. The herders, after spending the winter on the plain, left for the mountainous pastures during April and did not return to the plains until November, thereby avoiding the worst malarial seasons. Full-scale transhumance such as this would therefore alter disease patterns entirely. Halstead (1996) suggests that the Neolithic farmers practiced small-scale seasonal mobility, perhaps exploiting rocky slopes in spring and the marshy areas in late summer, in order to fatten the livestock for either consumption or for breeding. These limited population movements may, therefore, have caused herders to suffer

fewer infections than those who permanently occupied the site.

The introduction of domesticated animals, while increasing exposure of shepherds and herders to malarious areas, may also have altered infection rates significantly; the large number of domesticates, particularly cattle, may have deflected vectors which are both zoophilic and anthropophilic onto the animals (McNeill 1979; Saul 2003). *A. claviger* and *A. maculipennis* are good examples of such vectors, and in Macedonia, *A. superpictus* may also be included in this group (Lividas *et al.* 1941). The herd sizes are not possible to discern from the zoological remains; however, it is noted that ovi-caprine remains were better represented than cattle (Higgs 1962; Watson 1972). If these remains reflect the relative herd sizes, it is suggested that zoophilic behaviour would have been restricted, as sheep and goat have been shown to be less favourable to zoophilic vectors than cattle (Lividas *et al.* 1941). Nonetheless, the vector populations would have been attracted to the herds due to host odours and therefore to the vicinity of the human populations, potentially increasing the risk of infection (Bouma *et al.* 1995).

It is highly significant that even if the zoophilic vectors were diverted from humans, these vectors are often the least efficient. *A. sacharovi* and *A. plumbeus*, two highly anthropophilic vectors are not to be included in this category. These vectors are extremely receptive to all malarial parasites, highly anthropophilic and perhaps most importantly of all, are suggested to have been abundant due to the prevalence of their respective habitats: *A. sacharovi* being a brackish and saline-tolerant breeder and *A. plumbeus* being a sylvan vector. This would therefore suggest that the theory of zooprophylaxis, although potentially significant in tempering infection, would have had little to no effect upon the two vectors which may well have been the largest factors in malaria transmission and are suggested to have posed the greatest threat to the inhabitants of Nea Nikomedeia.

The population size of the settlement is worth considering with regards to the malariogenic capacity of the region. Nea Nikomedeia extends over 2.4 hectares and is suggested to have extended much further, the excavated area representing an estimated 8% of the entire settlement; should the density of the settlement reflect the layout of the entire site, it is estimated that the total number of dwellings could have approached 100 (Pyke 1996). Population estimates, which are based on these figures, vary considerably from 120 (Halstead 1981) to a maximum of 500-700 (Pyke 1996). The potential size of the host group is therefore unclear; however it is suggested that the host group was considerably larger than the population of Nea Nikomedeia, as excavations show that the plain of Veria was extensively settled throughout the Neolithic Period (figure 5.6) (Wardle 1983; Andreou *et al*. 1996; Wilkie *et al.* 1997). Several Early Neolithic sites lie in close proximity, largely based along the Aliakmon valley; Yiannitsa B, lying 25 km to the north east of Nea Nikomedeia is a contemporary site, as is Servia V, lying 500 m east of Servia and Goules-Varemenoi and Kranidia-Kryovrysi, both lying to the west of Servia (Ridley *et al.* 1979; Hondroyanni-Metoki 1990; Andreou *et al.* 1996). The majority of the sites in the vicinity of Nea Nikomedeia cover less than one hectare; however, rather than representing seasonal sites, many appear to have been permanent settlements, as evidenced by the construction of mud-brick houses (Andreou *et al.* 1996).

The valley is suggested to have been more densely settled than current archaeological evidence indicates, as the damming of the Aliakmon River during the 1970s led to inundation of the Aliakmon valley and the loss of many archaeological remains; Servia and Servia V for example now lie under several metres of water (Andreou *et al.* 1996). Surveys of the seasonally accessible lake terraces along the middle Aliakmon valley have revealed thirteen submerged Early Neolithic sites; however the damage to these sites is considerable and true estimations of their size are not possible (Hondroyanni-Metoki 1990).

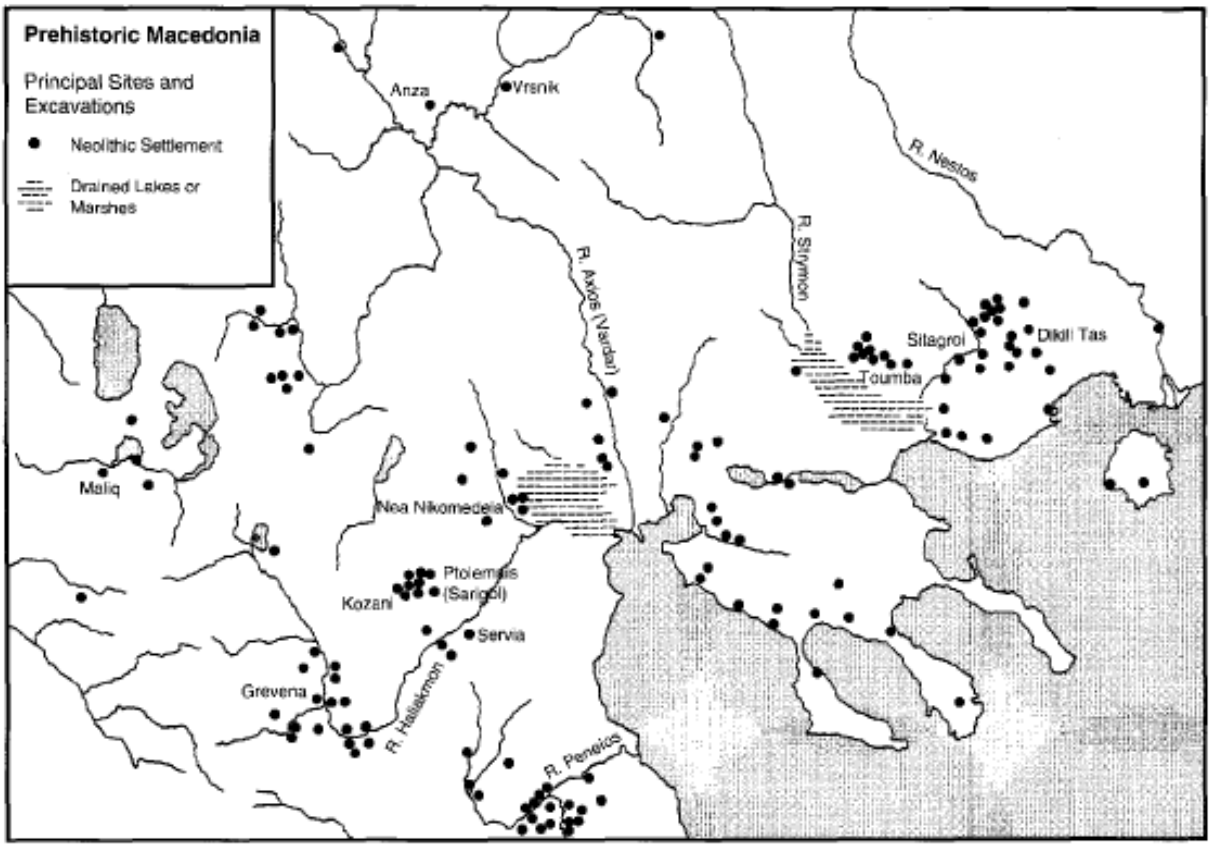


Fig. 5.6. Map showing settlements in the vicinity of Nea Nikomedeia. All sites within the Grevena region were occupied during the EN period (*After* Wardle 1983, fig. 9 and modified by Wilkie *et al.* 1997, fig. 1:pg. 202).

Further sites lie to the west of Nea Nikomedeia; surveys of the Grevena region have identified twenty Early Neolithic sites and while none have yielded radiocarbon dates, the material culture indicates that the sites are contemporary with Nea Nikomedeia (Wilkie *et al.* 1997). These settlements again occupy less than one hectare and the populations are therefore suggested to have been limited in size; however the occupation patterns, where the settlements are clustered along the river valley, have been interpreted as evidence that the river was used for both communication and migration, which may indicate that contact between the sites was a regular event (Wilkie *et al.* 1997).

It is worth considering here that these early farming communities from the east of Greek Macedonia are suggested to have been migrants from Thessaly; Wilkie *et al.* (1997) suggest

that the early Neolithic settlers followed the course of major rivers during their migrations from Thessaly and the Larisa basin. Contact with this region, either through migration or trade, is evident from pottery finds amongst the Early Neolithic sites at Grevena, Servia and Nea Nikomedeia; impressed pottery and evidence of white painted wares at Nea Nikomedeia were suggested by Rodden (1962) to be closely related to a primary settlement phase at Vrsnik in Yugoslav Macedonia, which would also suggest a possible link with the earliest verifiable food producing group from the Balkans. Transmission of this, or any diseases, would undoubtedly have been aided by these migrations and contact with these other population groups.

It is suggested therefore that the Aliakmon valley, and indeed the plain of Veria, was well settled during the occupation period of Nea Nikomedeia. The population of Nea Nikomedeia should not therefore be considered as an isolated host group, as contact between these sites would have been unavoidable as hunting, livestock herding, general landscape exploitation, trade and exchange would have entailed fairly regular contact between these settlements. Even if contact was irregular or only seasonal; modern malarial studies indicate that such contact would increase the host group and could transmit different clones of parasites, increasing the risk of infection (Bruce-Chwatt 1980; Freitas-Junior *et al.* 2000).

The malariogenic capacity of the site lies also in the construction of Nea Nikomedeia, which would have had important ramifications on disease patterns. The construction and layout of the site may have created viable *Anopheline* habitats; recent studies have shown that the construction materials, the layout and the quality of ventilation of the buildings, the proximity of livestock and the awareness of sanitation problems will determine the favourability of human dwellings for disease vectors and therefore have a strong influence on the vulnerability of the inhabitants (Lindsay *et al.* 2002; Ye *et al.* 2006). Excavations at Nea

Nikomedeia revealed three distinct building phases dating to the Early Neolithic with a total of twenty-four identifiable structures. The earliest of these phases revealed eight square and rectangular buildings of approximately 8.37 m by 6.66 m, suggesting that c. 4-6 individuals could have occupied each dwelling. One building with a presumed communal function was considerably larger (Pyke 1996). Two of these buildings contained internal partitions which divided the rooms into smaller, rectangular spaces and several of the structures have hearths, with ovens set against the outside walls (Pyke 1996). The second phase of construction is based on a similar layout, and is in fact built on the same orientation and again featuring a larger 'communal' building; however the number of internal partitions increases, forming multiple smaller rooms. The third phase revealed only six structures, but largely appears to follow a similar pattern as phase two. The limited extent of excavation has led Pyke (1996) to suggest a potential total of 100 structures for phase one and two and a total of seventy-five for phase three.

The malariogenic capacity of these buildings appears to have been considerable due to both the style of construction and the materials used. The walls were constructed of timber and reed frames which were plastered with mud on both the internal and external surfaces; floors were made of beaten clay or clay inlaid with pebbles, although the floor of the largest structure was made of mud overlying a 'matting' of marsh grasses and reeds (Rodden 1964: 564). There is no archaeological evidence for the structure of the roofs, but based on contemporary clay model houses found in Greece and the Balkans, it is suggested that the roofs were sharply pitched with wide eaves, and were most likely created with wooden frameworks and reeds, with perhaps a clay lining to insulate and waterproof the structure (figure 5.7) (Rodden 1964; Pyke 1996).

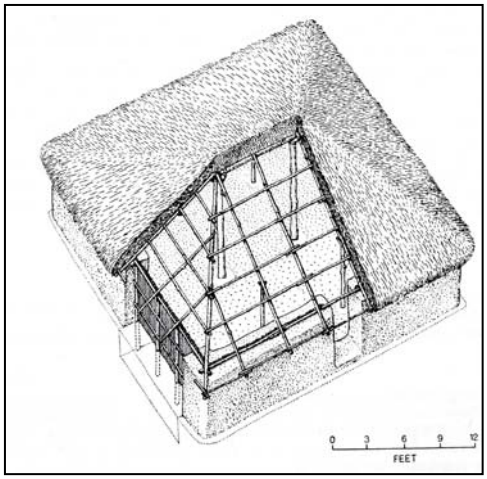


Fig. 5.7. Reconstruction of a house from Nea Nikomedeia *(After* Rodden 1965: 87).

Modern studies into the relationship between housing and *Anopheline* densities in northern Greece during the 1930s would suggest that these buildings would have rendered the inhabitants extremely vulnerable to infection; the materials used during the Neolithic are similar to those used during the early twentieth century, where roofs were often thatched and ceilings were often constructed of reeds (figure 2.11). These materials were proven to offer no protection against the vectors but were in fact attractive to the *Anopheles* mosquitoes (Barber *et al.* 1935). Mud-lined walls or roofs develop cracks as the mud dries; these, as well as gaps amongst the reeds and rushes, are well recognised as favoured shelters for *Anopheles* vectors as these niches provide both protection and cool, dark shelter during the heat of the day (Barber *et al.* 1935; Lindsay *et al.* 2002; Ye *et al.* 2006).

Despite the lack of evidence for roofs, it is possible to assess the dangers attached to these constructions, as any materials available to the Neolithic inhabitants would not have afforded much protection against the malarial vectors. Mud brick, grass, or wooden framed and thatched, all of the available materials would provide equally comfortable shelter for the *Anopheles* mosquito (Ye *et al.* 2006). A further danger linked to such structures is the ease with which the vector can enter the building, as the above materials all provide sizable gaps

which will permit the mosquitoes to fly in and out without disturbance (Ye *et al.* 2006). The wide eaves, suggested in Rodden's (1996) reconstruction of the houses, would be a particular danger. Lindsay (1988; *et al.* 2002) notes that such wide gaps expel 'host odours'; based on malaria studies in Africa, it has been shown that these odours attract the mosquitoes which will then simply fly through the gap to feed on unprotected and particularly sleeping people. These gaps can be blocked which will afford some protection; houses with closed eaves are noted to shelter far fewer vectors and infection rates are consequently far lower (Lindsay 1988; *et al.* 2002). Any attempts to block such gaps would only afford limited or temporary protection; however, if the materials were those with which the houses of Nea Nikomedeia were originally constructed. Renewal of the construction materials is evident in the archaeological record; the three construction phases noted at the settlement are suggested to have occurred in rapid succession which may have temporarily limited the accessibility of the houses to the vectors (Pyke 1996). The new constructions complete with fresh applications of mud and clay would limit the accessibility of the houses for the vectors; this would not however last for an extended period, as weather patterns, particularly the heavy rainfall patterns projected from palaeoclimatic reconstructions, would cause the building materials to deteriorate.

The style of construction and the choice of building materials, combined with the number of inhabitants would indicate that the endophagic vectors of the area would strongly favour such structures. The cracks would provide cool shelter during the heat of day and conversely, the small, partitioned rooms heated by the heat of human bodies and from a hearth, would provide warm and dry shelter during the colder conditions. This would potentially permit the vectors to survive and even feed during the winter months (Garnham 1948; Ye *et al.* 2006). The suggested proximity of the site to both brackish and fresh water would furthermore increase the probability that vectors would locate the dwellings.

Exposure to vectors at Nea Nikomedeia could therefore potentially have been possible twenty-four hours a day during the warmer months, as the economic activities of the day could expose the inhabitants to areas of high malariogenic capacity, while the construction and micro-environment of the dwellings would entice the vectors inside, making infection as likely as if the inhabitants slept outdoors.

Discussion

It is suggested that the historic endemic-epidemic cycle of transmission, which plagued the plain of Veria in more recent times, may well have applied to the Neolithic period and to the inhabitants of Nea Nikomedeia in a reduced capacity. The sheer diversity of the landscape and high volume of surface water indicates a significant malariogenic capacity, capable of supporting multiple vectors which would have permitted the infection season to be extended due to the differing life cycles of each species.

It is suggested that the climate of the Early Neolithic period would have limited this capacity to a degree, as the gradually declining winter temperatures during the early occupation of Nea Nikomedeia is likely to have resulted in markedly seasonal transmission; however the humidity levels, which remained high in relation to modern levels and elevated precipitation levels, would suggest a potential for extended vector life spans, increased biting habits, and augmented breeding grounds. This climate, combined with the high malariogenic capacity of the plain, is likely to have supported a long and intense transmission season (Lividas *et al.* 1941). The c. 200 year climatic deterioration of 8.2 ka BP may have been the exception to this, resulting in shortened, but more intensive, transmission seasons.

The vulnerability of the inhabitants to this malariogenic capacity is suggested to have been considerable; the settlement of Nea Nikomedeia, lying in close proximity to potentially

highly malarious waters such as the saline marshes and fresh water rivers, would have been vulnerable to *Anopheline* invasions. The living conditions of the settlement and especially the structure of the dwellings, would have afforded little or no protection against the invading vectors; equally the economic activities of the Neolithic inhabitants would have increased both the capacity of the landscape and the exposure of the early farmers to the areas of high malariogenic capacity. The risk of contact with biting vectors is therefore suggested to have been potentially continuous during the climatically viable seasons.

There are many social and environmental factors which would have limited the malariogenic capacity. Transhumance could have lessened exposure to the *Anopheline* vectors; most significant, however, is the limited areas of open land, which is suggested to have restricted the population density of many of the most virulent and efficient vectors, such as *A. superpictus* and *A. sacharovi.* It is proposed here, however, that the environment of the plain of Veria would have accommodated intense foci of these vectors, particularly along the saline meadows, coastal zone and on areas of cultivated land, which would have contributed to a malaria burden. The density of tree cover across the plain of Veria may equally have been a contributing factor to malarial transmission, increasing the habitat and abundance of *A. plumbeus* in the absence of other forest dwelling vectors. As abundance is recognised as a leading factor in transmission (Muirhead-Thomson 1951), it is suggested that this highly virulent and anthropophilic vector played a more important role than previously considered in early studies into the history of malaria.

A re-evaluation of the conditions surrounding Nea Nikomedeia therefore broadly concurs with Angels' (1973) theory that *P. falciparum* could have been transmitted on the plain of Veria during the Early Neolithic. The malariogenic capacity of the area, in so far as is it possible to ascertain, appears to have been high and there are no apparent climatic or

environmental reasons for any of the malarial strains, or *Anopheline* vectors, to have been absent. Although transmission would have been limited by colder temperatures following the 8.2 ka BP[95] event and smaller populations than those of the 1900s/1930s; the diversity of the landscape, highly varied water sources and elevated precipitation levels would be expected to result in a considerable malariogenic capacity in the locality of Nea Nikomedeia and to have placed a disease burden upon the Early Neolithic occupants. It is suggested, based on the palaeoclimatic and environmental reconstructions, that the malariogenic capacity of the Veria Plain was theoretically sufficiently high to result in the development of a genetic immunity.

[95] Commonly dated to 7400/7500 ^{14}C yr BP (Alley *et al.* 1997; Weninger *et al* 2006).

Chapter Six:

Palaeoenvironmental reconstructions: Malaria and the Bronze Age site of Lerna, Argive Plain

The site of Lerna is situated on the coast of the Gulf of Argos, within the Argive Plain in the Peloponnese. The osteological evidence from this site, cited by Angel (1971), entirely pertains to the Middle Bronze Age period (Middle Helladic I-II); however the reconstruction of the environment will encompass the entire Bronze Age occupation period of Lerna, from the Early Helladic II (EHII) in c. 2900 BC until the Late Helladic period (LH) in c. 1200/1180 BC (figure 6.1), due to a comparative lack of evidence for the environmental conditions of the Middle Helladic Period (Caskey 1960, 1968). Angel (1971) proposed, based on the osteological evidence, that the environment of the Argive plain during this period was extremely conducive to *Anopheline* vectors, despite a suggested climatic deterioration.

Modern malarial studies

Angel's (1971) contention was partly based on historical malarial studies from the past three centuries, which noted a high malariogenic capacity across the Peloponnese, and particularly the Argive Plain (Dodwell 1918; Stéphanos 1884; Lehmann 1937; Balfour 1935). The capacity was partly due to the diversity of the landscape which readily supported multiple vectors (Balfour 1935) (figure 6.2). The region is composed of a 243 km^2 coastal basin which opens onto the Gulf of Argos. Mountain ranges encircle the area; the Pindos zone, including the Artemision range lies to the west of Lerna at an elevation of 1772 m and steep hills surround the plain, varying from 400-700 metres high. The site of Lerna lies at c. 100 m from the western shore of the gulf and is surrounded by two fertile valley plains, the central plain lying to the north to north-east and a smaller plain lying to the south-west (Zangger 1993).

Relative Phase of the Bronze Age	Site Phase	Relative Chronological Phase	Chronological Period cal. BC (Manning 1995)	Lab Sample	^{14}C Age	Cal. BP σ 2	Cal. BC σ 2	Median cal. BC	Ref
Early Bronze Age	Lerna III	Early Helladic II (EHII)	2650/2450 -2200/2150	P-318 P-319 P-321 P-320 P-300 P-312 GrA-28046	4070±72 3980±66 3940±68 3930±65 3870±61 3840±72 3830±35	4821-4420 4798-4236 4569-4155 4528-4155 4437-4092 4430-3993 4408-4099	2872-2471 2849-2287 2620-2206 2579-2206 2488-2143 2481-2044 2459-2150	2638 2500 2428 2413 2346 2304 2283	(1,2,3)
	Lerna IV	Early Helladic III (EHIII)	2200/2150-2050/2000	P-303A P-299 GrA-28051 GrA-28213	3750±112 3750±97 3730±35 3640±45	4432-3831 4414-3877 4225-3977 4086-3846	2483-1882 2465-1928 2276-2028 2137-1897	2175 2173 2130 2009	
Middle Bronze Age	Lerna V	Middle Helladic I (MH)	2050/2000-1950/1900	GrA-28054 GrA-28045	3595±35 3585±35	4062-3779 3983-3731	2113-1830 2034-1782	1952 1940	
Late Bronze Age		(MHII)	1950/1900-1750/1720	GrA-28050 GrA-28039 GrA-28048 GrA-28041 P-303 GrA-28211 GrA-28157 GrA-28160	3560±35 3545±35 3535±35 3530±35 3520±59 3510±50 3475±40 3440±40	3970-3722 3959-3716 3907-3700 3898-3700 3970-3641 3913-3621 3842-3640 3831-3590	2021-1773 2010-1767 1955-1751 1949-1751 2021-1692 1964-1692 1893-1691 1882-1641	1909 1887 1865 1848 1844 1832 1804 1753	
		(MHIII)	1750/1720-1680	No radiocarbon samples					
		Late Helladic I (LHI)	1680-1600/1580						
	Lerna VI	LHIIA	1600/1580-1520/1480						
		LHIIB	1520/1480-1445/1435						
	Lerna VII	LHIIIA	1435-1360						
		LHIIIB	1360-1200						

Fig. 3.2c. Bronze Age occupation of Lerna, Argive Plain. *After* **1)** Kohler *et al.* 1961, **2)** Ralph *et al.* 1962, **3)** Voutsaki *et al.* 09. Calibrated with OxCal 4.1.

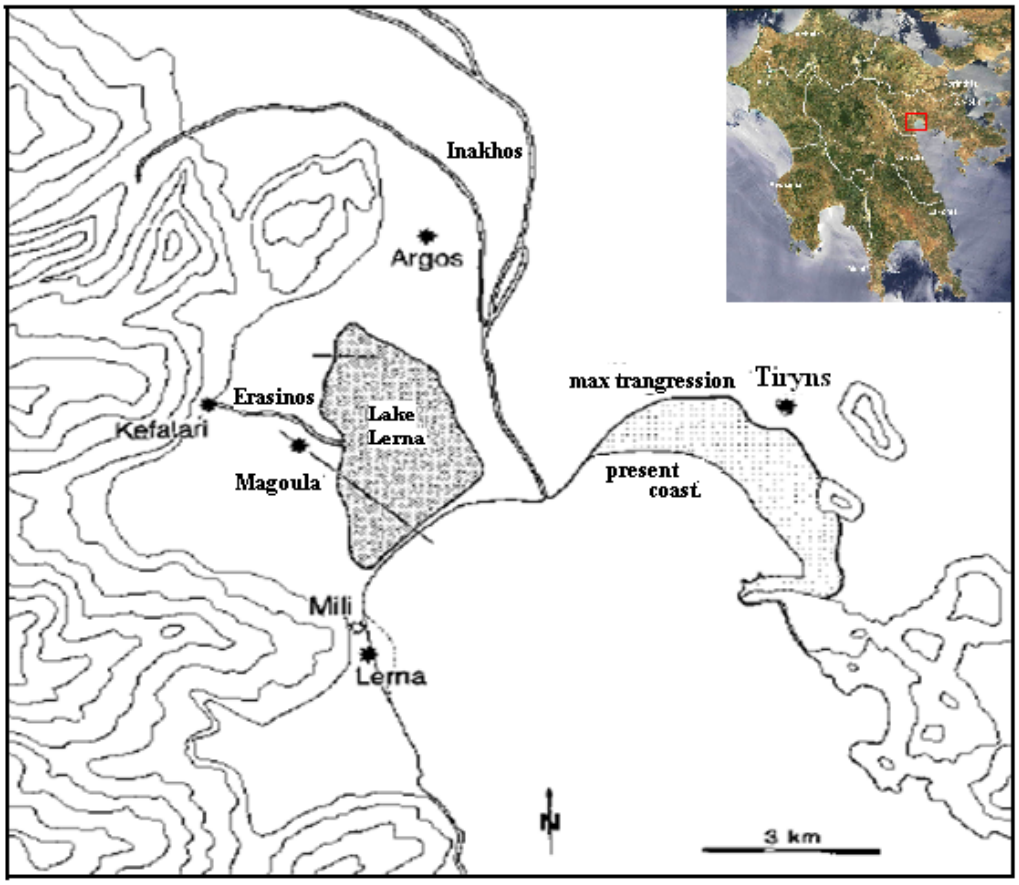


Fig. 6.2. Map of the Argive Plain, showing the coastal changes, rivers, springs and the position of Lake Lerna in relation to the site of Lerna (*After* Zangger 1991: fig. 5: pg. 7). Modified by author

The Argive Plain is a highly karstified region that is connected to Arcadia to the north; studies of the water systems of the Peloponnese show that surface waters absorbed by sinkholes in the latter region re-emerge on the Argive Plain (Higgins *et al.* 1996). Rainfall and snowmelt from the Pindos and Artemision mountain ranges are also absorbed and drained directly into the rivers and into the Gulf of Argos. The ephemeral river Inakhos and the perennial Erasinos River, one of the largest in the Peloponnese, both derive from these karstic systems and a smaller river, the Manessi, runs through the eastern plain, to the south of Tiryns. The Inakhos River is historically notorious for flooding; a severe event which occurs approximately every fifteen years, causing particular damage to Argos and other sites along the river (Zangger 1993).

The western section of the plain, in which Lerna is situated, is particularly well watered, creating an extremely green landscape in sharp contrast with the drier landscape of the eastern plain (Zangger 1991; Poulovassilis 1997). The flow of the Kephalari spring, emerging from the mountain side to the west of Lake Lerna, is highly active, feeding the perennial Erasinos River and numerous smaller karstic streams emerge across this section of the plain and along the coastline adjacent to Lerna (Higgins *et al.* 1996; Poulovassilis 1997). The quality and productivity of these streams was well noted in history; in the second century AD, Pausanius noted that while the rivers and other water sources in the Peloponnese would dry in periods of aridity, Lerna's karstic springs would continue to flow (*Description of Greece* 2.15.5). Travellers in more recent history, such as Dodwell (1819), also remarked on the activity of these streams. The western section of the plain has further been dominated by considerable areas of marshland in modern history, particularly in place of the ancient freshwater Lake Lerna, a water body that is no longer extant due to gradual natural infilling during, and subsequent to, the Late Bronze Age (Zangger 1991).

The diversity of the environment, combined with the abundance of water and the warm climate of the Argive Plain (see chapter three) has resulted in the notoriety of the region as a malarial centre throughout the past three centuries. Travellers have written of the unhealthy nature of the plain, describing the sickly appearance of the locals and the severe malarial fevers that afflicted the area (Dodwell 1819; Stéphanos 1884; Balfour 1935; Lividas *et al.* 1941). The frequency of the disease during the nineteenth century led Dodwell (1819) to suggest that the legend of the Hydra was linked to Lake Lerna and its malarious potential; the multiple karstic springs, or perhaps the many mosquito eggs of the *Anopheline* vector, representing the many heads of the mythical beast (Pausanias *Description of Greece* 2.37.4; Dodwell 1819; Zangger 1991).

The prevalence of the disease persisted in the region into the twentieth century; during the early 1930s, four sites from the northern Peloponnese were studied by Balfour (1935) and each was reported to have experienced moderate to high malaria endemicity. Three of these sites, Mourla, Temeni and Eghion, situated on the Gulf of Corinth, lay within coastal, marshy environments or in proximity to rivers, which resulted in a high prevalence of *Anopheline* vectors, with *A. sacharovi, A. superpictus* and *A. maculipennis* being the most established vectors. Although studies in the north of Greece debated the significance of *A. superpictus,* Balfour (1935) argued that the vector played a significant role in malaria frequencies in the Peloponnese, promoting a prolonged seasonal occurrence of malaria. Studies showed that the density of relative species, and therefore the prevalence of the disease depended entirely upon geographical location and quality of local water bodies; sites in close proximity (within 3 km) to coastal environments and marshland suffered particularly high densities of *A. sacharovi,* while rivers and "torrents" promoted greater numbers of *A. superpictus* (Balfour 1935: 308). The latter sites were therefore at a greater risk of late summer to autumn infection, while the former environments promoted earlier outbreaks of malaria; sites in proximity to both environments suffered from exceptionally long transmission seasons. *A. maculipennis* was the least frequent of the three vectors, although present within all of these environments; it was, however, the primary vector within inland plains (Balfour 1935). Other *Anopheline* vectors are not recorded in the northern Peloponnese in this study, as none were considered to contribute to the malarial burden in any significant manner. It is suggested here, however, that the bias towards these sun-loving vectors may have been due to the almost complete deforestation of the Argive Plain over the last century (Jahns 1993).

The combination of these three vectors resulted in high malaria morbidity, due to both the virulence of the vectors and the overlapping breeding periods. The moderate to high endemicity of the area furthermore led to a large percentage of the population harbouring two

malaria parasites, mainly *P. vivax* and *P. falciparum*, while "not inconsiderable numbers" were infected with all three parasites (Balfour 1935: 312). Malarial studies between 1900 and 1934 indicate that the combination of the three malarial strains accounted for 3.7% of the mortality rate within the Argolidocorinthia region between 1921 and 1935 and 36% of the morbidity rate (Balfour 1935; Lividas *et al.* 1941: 64).

Reconstruction of the malariogenic capacity of Bronze Age Lerna

Early Helladic II/ Lerna III (*2650/2450-2200/2150 cal. BC/ 4600/4400-4150/4100 cal. BP*)

Early reconstructions of the environment of the Argive Plain suggested that the central plain was composed of marshland throughout the prehistoric period, which would have been highly conducive to malaria (Angel 1971). Based on geological studies which noted the prevalence of karst basins and impermeable clay soils, these reconstructions indicated that extensive areas of marshland surrounded the springs, streams and the coastal estuary (Stéphanos 1884). This was supported by historical records; Aristotle noted that the region had a small carrying capacity due to water logging, as "at the time of the Trojan war the land of Argos was marshy, and could only support few inhabitants" (*Meterologia* 14.325, *translated by* Schliemann 1885: 29). This theory, on which Angel's (1971) hypothesis of high malariogenic capacity was partly based, was confirmed by later geomorphological studies. Bintliff (1977) proposed that the plain remained highly waterlogged until c. 1500 years ago, when a single severe case of soil instability, termed the Younger Fill, began to backfill the marshy areas. Bintliff (1977) therefore concluded that extensive marshland limited the agricultural capacity of the plain and that the economic emphasis of Bronze Age Lerna focused on the cultivation of the soils of the hill zones and on marine resources.

The theory, and therefore Angel's (1971) environmental analysis of the plain, is now considered erroneous; subsequent geomorphological studies have shown firstly, that multiple alluvial events affected the plain, all of which occurred far earlier than Bintliff (1977) suggested (Zangger 1993). Sediment analysis shows that the first of three alluvial events occurred during the Late Neolithic/ Early Bronze Age (between approximately 4500 BC and 2500 BC)[96]; the extent of the soil deposition is unknown, however deposits were identified near Magoula (to the north of Lerna) and along the coastal plain. Secondly, core analysis indicates that the surface of the coastal plain was stable after the initial deposition, with marshland only predominating along the backshores; no evidence of widespread waterlogging was found and the soil composition indicates human use, leading Zangger (1993) to suggest that these soils were as secure, and as suitable for cultivation, as the modern soils. Geomorphological studies would therefore indicate that the Early Bronze Age landscape was never as marshy as first suggested (van Andel *et al.* 1990a,b; Zangger 1991; 1993).

Angel's (1971) hypothesis of a high malariogenic capacity remains viable however; geomorphological studies indicate that the rivers, Erasinos and Inakhos, and the karstic springs were active during the Bronze Age. These are suggested to have produced patchy areas of marshland along the lake edges, in occasional pockets across the plain and along the coastal zone (van Andel *et al.* 1990a,b; Jahns 1993; Poulovossilis 1997). This is supported by pollen frequencies taken from a single sediment core from Lake Lerna, lying at approximately one kilometre to the north of the site of Lerna. The pollen data indicate high but fluctuating frequencies of marshland taxa after 3600 cal. BC (5550 cal. BP)[97] (Jahns

[96] The exact date of this event is unknown, however a Middle Neolithic site is buried by the alluvium and a radiocarbon date from the succeeding context provides a *terminum ante quem* of 2567 cal. BC (4047±155 ^{14}C yr BP/ 4517 cal. BP) (Zangger 1993)
[97] 4800 ^{14}C yr BP (Jahns 1993)

1993), including *Sparganium* (bur-reed), *Poaceae* (wetland grasses), *Cyperaceae* (sedge-grass), and *Typha latifolia* (bulrushes) (figure 6.3). Sedge-grass is particularly prevalent throughout the Bronze Age, signifying a constant presence of heavily waterlogged and marshy soils around the coring site (Jahns 1993).

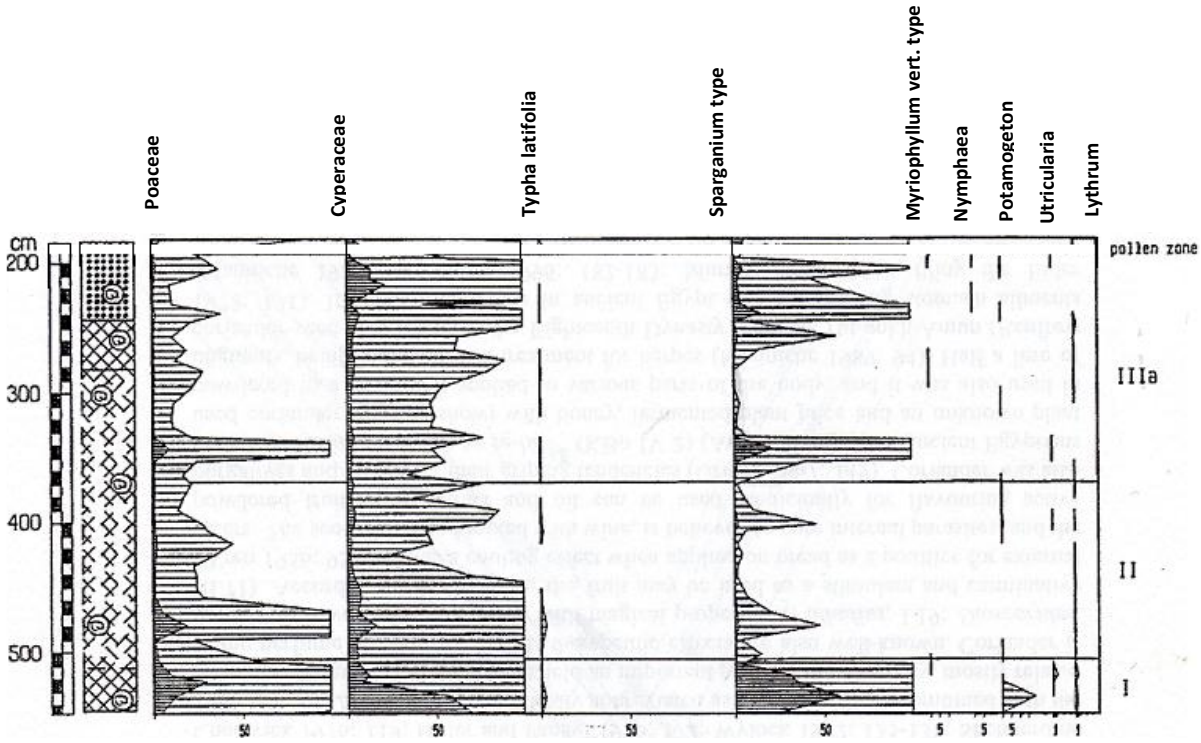


Fig. 6.3. Marshland taxa frequencies from Lake Lerna core. Seven radiocarbon dates provide a uniform sedimentation curve of 0.75 mm per year, allowing an approximation of the ages of the pollen zones. The Bronze Age occupation is represented by zone IIIa, dated from 3600 cal. BC/ 5550 cal. BP (4800 ^{14}C yr. BP) to c. 1010 BC/2960 BP (interpolated) (*After* Jahns 1993; fig.7: pg. 198). Modified by author.

Although the landscape is not as extensively waterlogged as suggested by Angel (1971) and Bintiff (1977); the core from Lerna would indicate a high volume of marshland and therefore a high capacity for *Anopheles* breeding grounds. The malariogenic capacity would have been augmented still further by the fresh waters of Lake Lerna; fed by many ephemeral karstic springs and the perennial Erasinos, sediment cores indicate that this lagoon was shallow but wide during the Bronze Age, extending for approximately 4.5 km (Jahns 1993; Zangger 1993). The identification of fresh water ostracods within these sediment cores indicate that

the waters of Lake Lerna remained fresh throughout the Bronze Age[98], despite its extreme proximity to the sea; this was due to a substantial sand barrier constructed by sediments deposited by the Inakhos River which prevented saline water influxes (Zangger 1991; 1993).

The volume and variety of water bodies in the region are suggested to have provided viable and extensive malarial breeding grounds for all the vectors in question. Most significantly, the primary vectors of Greece could have been supported by these water bodies. *A. sacharovi*, favouring stagnant, shallow or saline water, is suggested to have predominated along the coast and the lake; references to the studies conducted by Balfour (1935) at sites along the Gulf of Corinth would suggest that the marshland surrounding Lake Lerna would have strongly favoured this vector. The same study may be used to indicate that the geographical position of Lerna, lying at the foothills of the mountains to the west and in proximity to the lake and the multiple karstic springs, may have resulted in a high capacity for *A. superpictus*, while the lake, especially the areas surrounded with fringes of overhanging vegetation would also have supported *A. maculipennis.* These environments would also, theoretically, have favoured some secondary and other, rarer, vectors; including *A. atroparvus, A. hyrcanus* and *A. claviger* (see chapter 2) (Becker 2003). The hydrological systems of the Argive Plain are therefore suggested to have provided a high malariogenic capacity for multiple vectors, and a high water availability which may have mitigated the unfavourable climatic conditions following the termination of the HHP (see chapter 3).

Early Helladic II further coincided with a eustatic sea level rise, culminating in a marine transgression onto the eastern portion of the inner plain; the coastline reached its northernmost point in c. 2500 cal. BC (4450 cal. BP)[99] (figure 6.2) (Zangger 1993; 1994; van Andel *et al.* 1990c). Marine seismic investigations and sediment cores indicate that coastal

[98] Dated through diagnostic pottery sherds (Zangger 1991).
[99] 4027±155 ^{14}C yr BP (Zangger 1993)

outbuilding began immediately due to sediments carried by the river Inakhos; this resulted in a gradual regression of the coastline, which reached the modern level in approximately LHIIIB (Kraft *et al.* 1977; van Andel *et al.* 1980; van Andel *et al.* 1990c; Zangger 1991; 1994). These environmental changes would have resulted in several alterations in potential mosquito breeding grounds, particularly on the inner plain; the height of the transgression during EHII caused much of the eastern area of the Argive plain to be inundated with both fresh and salt water, forming further breeding grounds for vectors tolerant of brackish water. The western coastline was, however, largely unaffected by these changes and remained within approximately one hundred metres of Lerna, which would indicate a potential for brackish breeders to oviposit within flying range of the site (Zangger 1993).

The tree cover of the area was also favourable to the majority of the proposed vectors. Pollen cores from Lake Lerna indicate that the landscape was fairly densely wooded prior to c. 3600 BC (5550 cal. BP)[100] when human impact is gradually manifested (Jahns 1993). Oak woodland cover steadily decreased while the frequency of *Artemisia* and Chenopodiaceae, indicators of disturbed habitats, maquis vegetation, such as *Erica* (L.) (heather), *Phillyrea* (L.) (mock privet) and *Olea*, and light-demanding trees, such as *Corylus* increased (figure 6.4) (Jahns 1993). After c. 2500 cal. BC (4450 cal. BP)[101] an increasing frequency of ruderals, such as *Plantago lanceolata, Polygonum aviculare* (common knotgrass) and Amaranthaceae taxa, indicate an increase in farming and expanding pasture land (Jahns 1993). By the beginning of the Early Bronze Age, the pollen data suggest that the plain was a mosaic of open woodland, maquis, phrygana and areas of pasture; the limestone slopes were most likely barren, as they are today, with areas of maquis clinging to the surface. Pasture

[100] 4720 ^{14}C yr BP (Jahns 1993)
[101] 4000 ^{14}C yr BP (Jahns 1993)

land and cultivated areas, fringed by open woodland and patches of maquis, would have covered the plains, while coastal meadows would stretch to the sea (Jahns 1993).

The progressive increase in forest clearance would have had strong effects on *Anopheline* habitats, increasing local temperatures and the prevalence of sunlit water bodies and reducing water absorption capacity of the soils. This combination of factors is suggested to strongly favour the primary vectors of modern Greece, creating conditions suitable for increased breeding grounds and augmented population densities (Patz *et al.* 2000; Leishout 2004; Yasuoka *et al.* 2007).

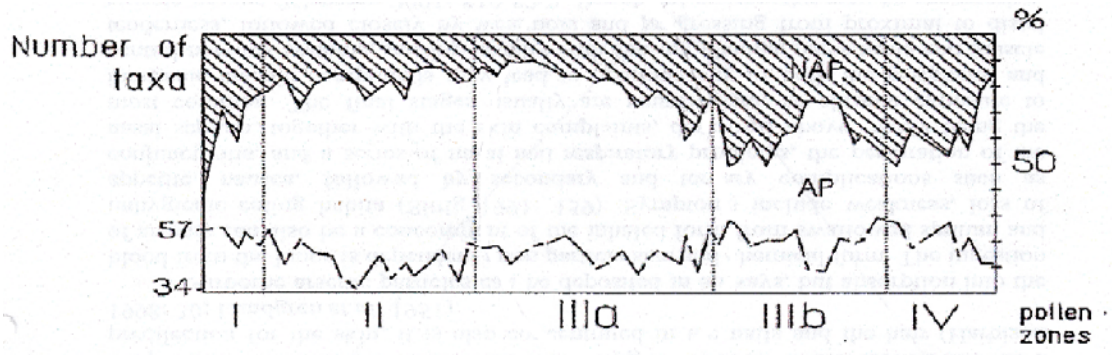


Fig. 6.4: Arboreal pollen (AP) and non-arboreal pollen (NAP) frequencies from Lake Lerna core. Pollen zone II is dated to the Neolithic 6330 BP (interpolated). IIIa represents the Bronze Age, beginning in 3600 cal. BC/ 5550 cal. BP (4720 ^{14}C yr BP) and ending in c. 1010 BC/2960 BP (interpolated) (*After* Jahns 1993; fig. 10: pg. 201).

The increase in anthropogenic activity across the plain is linked to the considerable peak in settlement density during the Early Helladic period. The EHII settlement at Lerna was prosperous, with an estimated maximum population of 800 (Caskey 1968; *et al.* 1997). The site was far from isolated however, as the Argive Plain was particularly heavily occupied, perhaps due to the fertile soils and high water availability of the region. The EHII settlement at Lerna was contemporary with the local sites of Magoula, Argos, Tiryns, Mycenae, Asine, Midea, and Nauplion (Wiencke 1989). Intense surveys of the Southern Argolid, Nemea and Berbati-Limnes regions have found a similar peak in settlement density, indicating that the

EHII period was one of population nucleation; not all of these sites are large, some covering just 1 ha, however, some are more substantial, covering 2-3 ha (Wells *et al.* 1990; Jameson *et al.* 1994; Cherry *et al.* 2002). The potential host group for the transmission of malaria, and other density dependent diseases, was therefore considerable, as contact between these settlements, through political, social and economic ties would have been extremely regular (Wiencke 1989). (The implications of widespread contact with other population groups and of the trade relations that emerged during the Bronze Age will be considered separately below due to the relative complexity of the subject).

The intensification in settlement patterns and land use initiated the development, or adoption, of new agricultural technologies, which modern malaria studies indicate would alter the viability of the land for the more virulent *Anopheline* vectors (Yasuoka *et al.* 2000). It is suggested that the plough would have been introduced by this period, and the discovery of terracotta figurines of an oxen and plough at Tsoungiza, Nemea, provides a *terminus ante quem*[102] of EHII (Pullen 1992). This would indicate that agricultural practices could have been applied on a far larger scale than previously possible, permitting the cultivation and exploitation of new areas, particularly, upland regions (Pullen 1992). Greater areas of the landscape may therefore have been open and sunlit, again indicating an increasingly viable environment for the survival and reproduction of the primary vectors (Yasuoka *et al.* 2007).

Ploughing can, however, reduce water availability; even with a simple ard, the act of ploughing will break up and remove the surface crust layer, increasing the permeability of the soils. The frequency of water-filled depressions within the soil surface would therefore be reduced or, at least, the time for which the pool persisted would be decreased (Gianotti 2008).

[102] Sherratt (1981) argues that the plough had been introduced into the Aegean from Asia Minor by c. 3400 BC (c. 5550 BP). It should be noted, however, that no evidence survives and no plough marks have been preserved in the archaeological record.

Ploughing would therefore limit the volume of surface water within cultivated fields, and therefore could, theoretically, reduce the exposure of the agricultural labourers to the *Anopheline* vectors.

The cultivated regions must, however, have been located in proximity to water; there is no archaeological evidence for irrigation systems, suggesting that the karstic springs and rivers were used to water the crops. The pollen data indicate that einkorn, emmer wheat, barley, lentils, vetch, peas, grape, flax, olive and *Vivia faba* (L.) (fava) were cultivated (Hansen 1988); crops which are likely to have been based on alluvial soils close to the waterways, which would be fertile, well-watered and well-drained (Hansen 1988; Oplinger 1989; Wainwright *et al.* 2004). This would place the agricultural labourers in close proximity to high volumes of water and to potential breeding grounds of the primary and secondary *Anopheline* vectors. It is also noted that the increasing cultivation of *Olea* (olive trees) may have supported *A. plumbeus* populations; olive trees are well known as potential breeding grounds for this species, along with oak, beech, elm and lime (Blacklock *et al.* 1920a; Lividas *et al.* 1941; Becker *et al.* 2003).

The effects of the high malariogenic potential of the area upon the inhabitants would naturally depend upon their use of the landscape; in conjunction with agricultural activities, it would appear that the highly varied landscape was widely exploited for wild resources. Data pertaining to the diet of the early Helladic (EHII) occupants of Lerna indicate that c. 22% of the meat assemblage was wild. The woodlands were particularly exploited as *Sus scrofa* (L., 1758) (wild boar), *Bos primigenius* (Bojanus, 1827) (aurochs), *Canis lupus* (L., 1758) (wolf) and red deer were hunted (Gejvall 1969), suggesting that woodland habitats were in close proximity to the site. This is suggested to have exposed the hunters and potentially the site of Lerna to the virulent *A. plumbeus* (Becker *et al.* 2003). Animal husbandry was however

particularly emphasised; Gejvall (1969) indicates a systematic breeding of domestic pig, sheep, goat and cattle. Goat appears to have been particularly prevalent, while cattle are suggested to have been the most important domesticate, perhaps due both to meat production and to their use as draft animals for ploughing (Gejvall 1969; Pullen 1992).

The areas in which the livestock were maintained are likely to have had a high malariogenic capacity; grazing sheep and cattle require open and well watered areas, and the grazing pressure can help to maintain an open landscape, thereby increasing the malariogenic capacity for the sunlight-loving primary vectors. Cattle grazing, or watering along streams, can furthermore reduce the volume of overhanging vegetation, which will again increase the favourability of water bodies for the primary vectors, as well as for the secondary vectors, *A. atroparvus* and *A. claviger* (Becker 2003). Water-filled cattle footprints are notoriously favoured by these vectors (Sabatinelli 2002), and have been considered as the main cause of increasing *A. superpictus* populations in Israel (Pener *et al.* 1985). It is suggested that the farmers would have been intensively exposed to this landscape; livestock require vigilant shepherding to both maintain the flocks and to protect them against the predators of the area, such as the wolves that were noted in the faunal assemblage (Gejvall 1969). Practices such as sleeping outdoors in order to guard the flocks, commonly practiced during the early twentieth century, would have increased the risk of infection further (Jones 1909).

The landscape of the plain was, however, significantly altered during the Early Helladic period. A major phase of soil instability, dated to 2800-2350 BC by diagnostic potsherds resulted in an abrupt phase of alluviation, which transformed the geography of the plain, the coastline and the lake (Zangger 1993). It is suggested that this alluvial event was partly initiated by heavy precipitation; sediment cores from the alluvial fans of the Inakhos River revealed interbedded gravels and loams overlying a cobble base, indicating a high energy

discharge and extension of the fans, far beyond that noted for the Neolithic period. This would suggest that these heavy river discharges were not only abundant but were also sustained (Zangger 1993). The increasing deforestation of the surrounding hills would also have increased the risk of soil instability; once the slopes and hills are denuded of vegetation, episodes of heavy rainfall can strip the topsoil (van Andel *et al.* 1990). Reconstructions from auger cores indicate that metres of fertile top soil were stripped from the foothills to the north, northwest and the east of the Argive plain and deposited along the stream courses, across the plain, and to a greater extent along the coastal strip, causing the coastline to slowly prograde (figure 6.5) (van Andel *et al.* 1990a,b; Zangger 1993; 1994). The duration of the event is uncertain; however the sedimentation rate indicates that the environmental change was "drastic" (Zangger 1993: 52).

This event would have markedly altered the malariogenic capacity of the area. The breeding grounds along the central and eastern area of the plain would have been affected, as the newly deposited soils would have buried pools of waters along the rivers, streams and coastal marshes. Transmission would have been temporarily disrupted by such large scale changes to the breeding grounds; however, the newly deposited alluvial soils along the stream banks would have become heavily water logged after subsequent rainfall, as the absence of root systems or plant litter would lower the water absorption rate. Further breeding grounds would, therefore, have been created fairly rapidly once the new soils had settled. It is also suggested that the loss of top soil along the higher upland regions would have caused subsequent rainfall to pool and run off the surface; this may have resulted in further water pooling along the plain. These changes would, therefore, indicate that extensive breeding grounds would have developed across the plain, and as mosquitoes are quick to adapt given viable conditions, the potential for water logging would suggest a high malariogenic capacity and the potential for rapid colonisation (Patz *et al.* 2000).

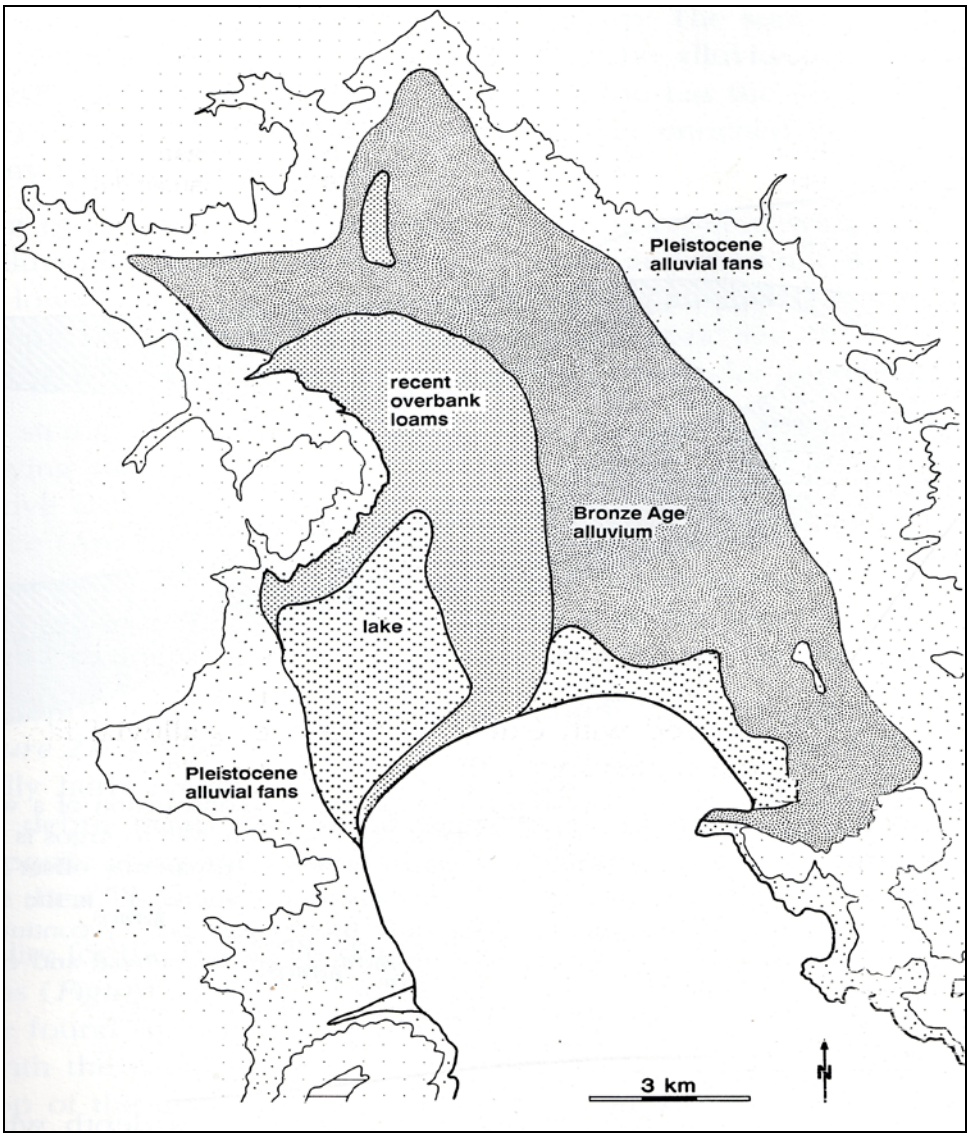


Fig. 6.5. Map of the Argive Plain showing the EHII (Early Bronze Age) alluviation event (*After* Zangger 1993*:* fig. 21: pg. 37).

The strongest effects of this event were undoubtedly felt by Tiryns and Argos and it is suggested that the malariogenic capacity of these settlements following this event was extremely high. The distribution of the alluvial soils would not have directly affected Lerna; the lake, however, was strongly affected, as approximately 3 metres of topsoil was deposited into the lake (figure 6.6) (Zangger 1993; 1994). Sedimentary studies from a trench positioned to the north of the lake, just south of Argos, indicate that the western area of the lake was less

affected than the eastern, remaining open until more recent history; the eastern part, however, was infilled by this event, which is again dated by diagnostic sherds to EHII (Zangger 1993; 1994). The lake was reduced both in size and depth (Zangger 1994).

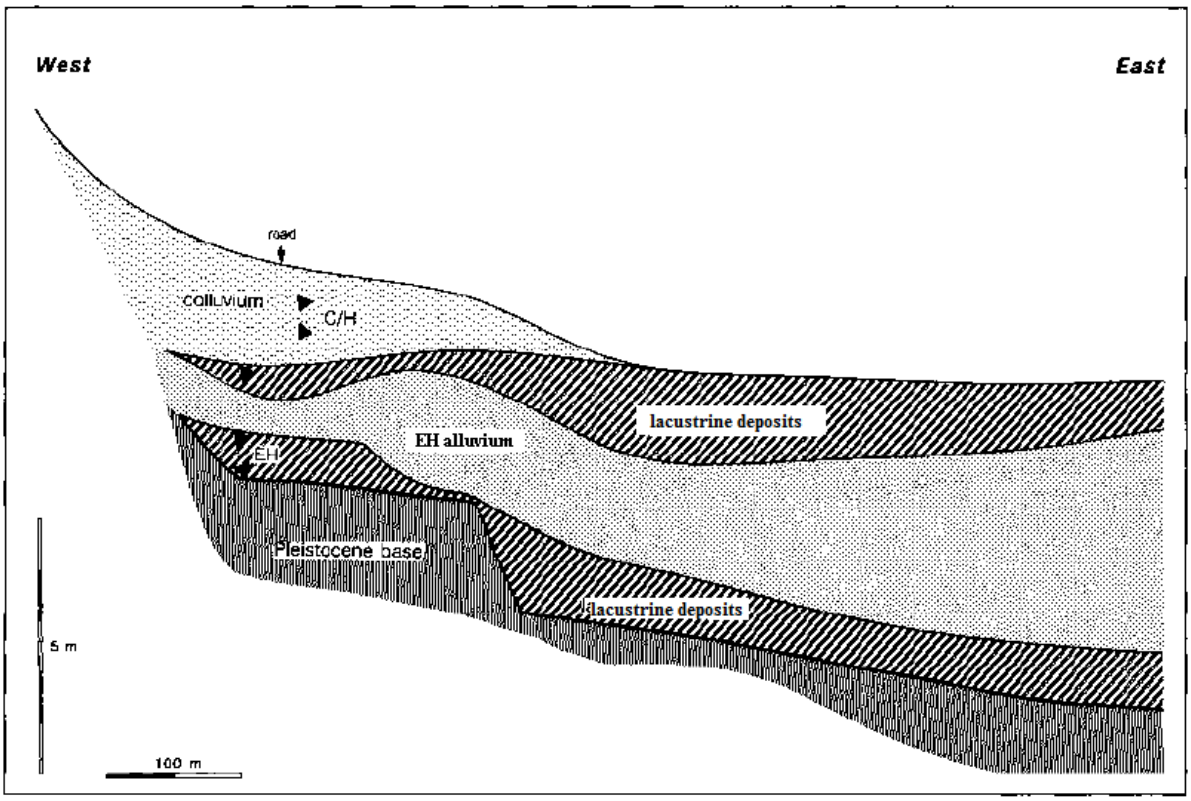


Fig. 6.6. Cross section of a trench placed in the north of Lake Lerna, showing the extent of the EHII alluviation event. The date of the second lacustrine deposit is unknown; however the eastern section of the lake is suggested to have remained shallow subsequent to deposition of 3 m of alluvium in EHII. The colluvial event dates to the Helladic Period (*After* Zangger 1991: fig. 8: pg. 12).

This would indicate that the volume of marshland, heavily waterlogged soils and shallow pools of water around the lake would have increased; changes which modern studies indicate would strongly favour *A. sacharovi, A. superpictus* and *A. maculipennis*, as well as secondary vectors such as *A. algeriensis, A. atroparvus, A. claviger* and *A. melanoon* (Becker 2003). Balfour's (1935) study of *Anopheline* frequencies in the Argolidocorinthian region would indicate that *A. sacharovi* and *A superpictus*, vectors which particularly favour marshy areas and stagnant water (although *A. sacharovi* will not tolerate eutrophic waters), would become

increasingly prevalent with such changes in water availability. Modern examples of such environmental changes suggest that this combination of events, occurring during a period of higher temperatures and in relatively arid conditions (see chapter three) would be extremely dangerous; gonotrophic and sporogonic cycles would be quickly completed under warmer temperatures, so that any environmental changes accompanied by an increase in viable breeding grounds, could result in sharp increases in transmission (Bouma 1994a,b; Lindsay *et al.* 1996a; Leishout *et al.* 2004). The alluviation event and subsequent alterations to the rivers and lake would have had a significant impact on the malariogenic capacity in the locality of Lerna; any increases in vector species in the environs of the lake, which lay at barely 1 km from Lerna, would be followed by invasions into the settlement and houses, especially by endophilic vector species.

The settlement of Lerna is suggested to have had particular repercussions on transmission patterns, potentially helping to maintain infection rates throughout the Early Helladic period. In comparison with the settlements previously considered in this study, EHII Lerna was a large and complex settlement (Caskey 1954; 1957; 1960; 1968), which is suggested to have provided substantial alternative habitats for the *Anopheline* mosquitoes that favour urban habitats (Bruce-Chwatt 1980). The site, expanding over approximately 1.2 to 1.5 hectares, would have supplied an abundance of breeding grounds in the form of wells, cisterns, drains and pools of water within the urban fabric. The perennial provision of water bodies provided by these urban societies would effectively ensure the presence of breeding grounds in close proximity to the inhabitants, while human dwellings and animal shelters would provide protection against climatic conditions.

During EHII the site appears to have flourished, becoming an important local ‘palatial and military establishment’, complete with substantial fortifications and ‘monumental’ buildings

(figure 6.7) (Caskey 1960; 1986: 20). The architecture, combined with evidence for prestige goods and craft production, indicates considerable social and economic complexity (Wiencke 1998). The size of the site is uncertain, as only 10% of the site has been excavated (Wiencke 2010) and the number of households is therefore not easily identified; however, data suggest between 30 and 110 households with the larger proportion of these houses being rather small (Caskey 1954; 1957; 1960; 1968).

The materials of these buildings are particularly significant with regards to potential infection rates. The majority of the walls were constructed of packed clay and unfired bricks, although some used limestone slabs, while roofs were constructed of schist[103]; it is however suggested that some may have been thatched (Caskey 1957; 1960; 1997). The roof of the famous House of Tiles suggests that some may have been constructed of well-fired overlapping tiles on gently pitched roofs (Caskey 1957; 1960). It should be noted however that this building is not suggested to have served a domestic purpose, but perhaps more of an economic or social function; it is included, however, to give a fair representation in the choice of materials and building techniques of the domiciles of Lerna.

The efficacy of these materials with regards to mosquitoes is varied; limestone slabs would limit vector access, however, mud brick walls are notoriously linked to high infection rates as mud and clay will develop cracks and will subside over time, providing niches for the vector and permitting access into the dwelling (Ye *et al.* 2006; Kirby *et al.* 2008). One building was constructed with a metre thick wall which would provide greater protection against vectors; however the dimensions appear to be an exception rather than the rule (Caskey 1960).

[103] Medium to coarse grained metamorphic rock composed of laminated, often flaky, parallel layers.

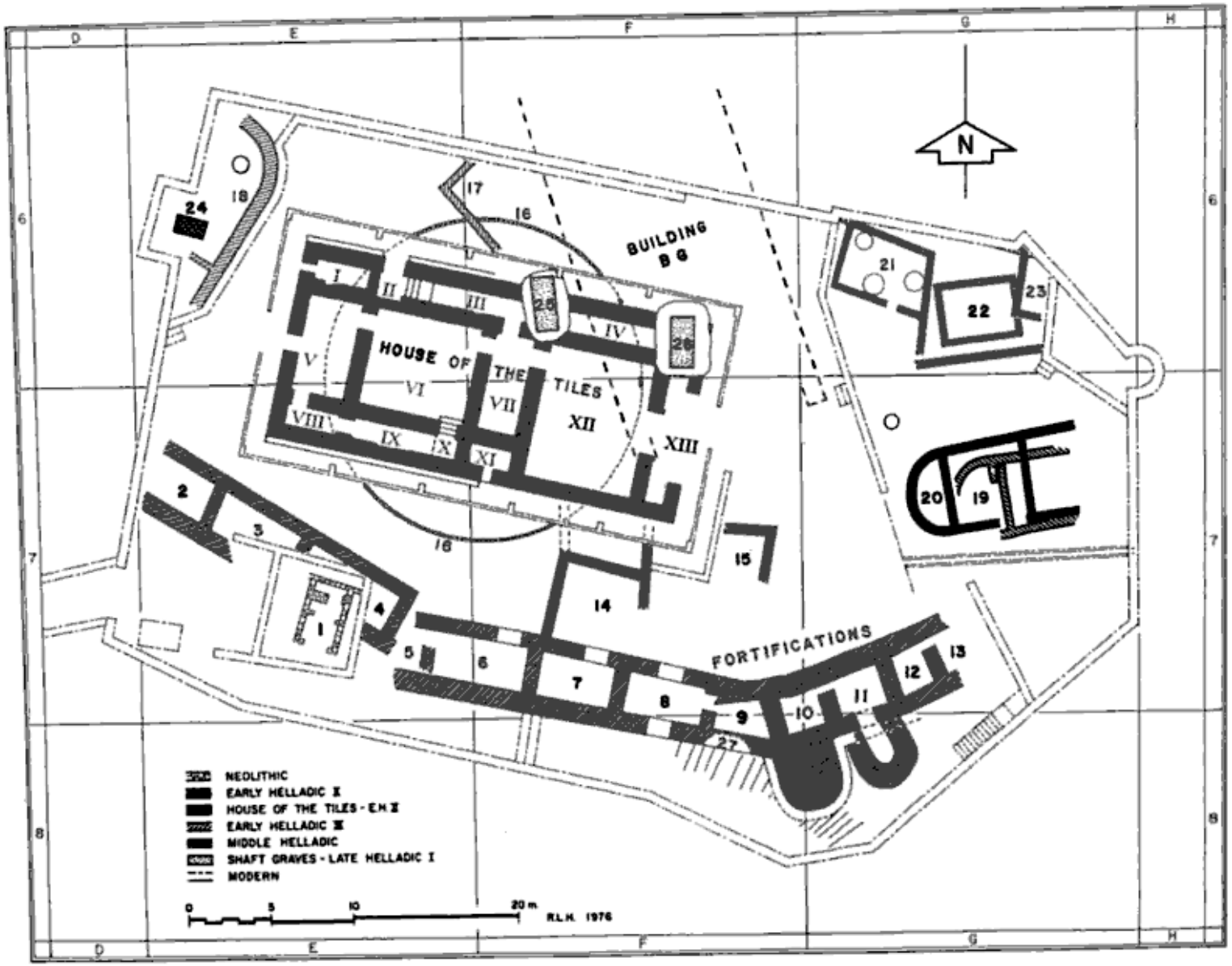


Fig 6.7. Plan of the main excavated area of Lerna (Caskey *et al.* 1997: fig. 1: pg. 2).

It is apparent that other materials were known of and used; some inner walls of the House of Tiles were covered with lime plaster which, if applied to the general dwellings, would have been far more effective against nocturnal mosquitoes than mud brick. The light colour of the plaster is recognised to be less attractive to the *Anopheline* vectors than dark mud walls (Caskey 1968; Lindsay *et al.* 2002; Ye *et al.* 2006; Kirby *et al.* 2008). There is, however, no evidence for such a practice amongst the 'average' buildings, but as the materials were available, it may have been a material of common usage (Caskey 1968). The roofing materials were equally varied in efficiency; thatch offers little to no protection against mosquitoes and the inhabitants could therefore be expected to be at some risk of infection. The well-fired tiles and schist, however, would protect the inhabitants considerably more efficiently. Other significant factors in indoor nocturnal infection rates are not evident; the number of occupants, the presence of domesticated animals and the width of eaves are all important factors but are not possible to reconstruct from the available archaeological evidence (Ye *et al.* 2006; Kirby *et al.* 2008).

The indication is therefore that many of the materials used are largely inefficient at preventing vectors from entering the domicile; high infection rates would be expected, as the inhabitants slept in mud-brick and thatched houses within 1 km from a freshwater lake and marshes and within several hundred meters of the coastline and coastal marshes (Zangger 1993). It is apparent, however, that construction materials had become more varied and sophisticated than those of the Neolithic; the use of limestone, schist and tiles in some of the houses would have afforded greater protection and potentially have minimised nocturnal infections.

EHII at Lerna ended in c. 2050/2000 BC (Manning 1995) with dramatic destruction, as catastrophic fires swept through the site, destroying the dwellings and the famous House of

Tiles. The cause of the destructions at Lerna is still debated; Caskey (1960) proposed that this event was contemporary with destructions at Tiryns, Asine, Kolonna, Zygouries, Agios Cosmas and possibly Corinth, and concluded that violent occurrences, such as foreign invasions were the cause. This is no longer considered a viable theory; subsequent advances in dating have shown that destruction levels vary temporally, many occurring in EHIII rather than EHII (Rutter 1993; Forsèn 2010). Regardless of the exact cause or geographical scale of the devastation, modern malarial studies would indicate that such events are linked to a deterioration in living conditions, which will dramatically alter the malariogenic capacity of the locality (Bruce Chwatt 1980; Watson *et al.* 2007). Caskey (1968) reports, however, that excavations uncovered no completed houses contemporary with the fire destructions at Lerna and suggested that the entire site was being rebuilt at the time of destruction. If this was the case, we would presume that the inhabitants were perhaps in temporary or unfinished dwellings. Rebuilding phases, like phases of destruction, are likely to increase infection rates as temporary dwellings rarely offer sufficient nocturnal protection and overall living conditions are often poor. Fire destruction would, nonetheless, effect dramatic changes on disease patterns, as violence and poor living conditions can increase the vulnerability of the local inhabitants to infection, as immune systems will weaken with shock, hunger or through living in poor conditions (Bruce Chwatt 1980; Watson *et al.* 2007).

The climatic, environmental and social conditions of Lerna during EHII would therefore appear to have been highly conducive to both the *Anopheles* vector and the malaria *Plasmodiae.* The general climatic trends (see chapter three), particularly the declining humidity levels following the end of the HHP, may have marginally reduced the malariogenic capacity of the plain; however, the vast diversity of the landscape and exceptionally high volume of surface water along the western and central plain, would create a rich variety of micro-habitats, resulting in a high potential for numerous vectors to coexist within the region.

The potential for malarial transmission is suggested to have been augmented by the increased population density in southern Greece and the resultant intensification of anthropogenic activity; this would have not only created a high malariogenic capacity but also led to high and prolonged exposure of the Early Helladic populations to these areas. Deforestation and cultivation of the plain would have strongly favoured *A. sacharovi, A. superpictus,* and *A. maculipennis,* indicating a capacity for long transmission seasons; thus the proposed capacity of this landscape, combined with the increased size of the host group, would indicate a higher potential for malarial infection (Balfour 1935; Lividas *et al.* 1941). The increasing sophistication of the urban developments of the Bronze Age is likely to have provided protection against environmental or climatic disasters, creating favourable and stable microenvironments for the vector species within the confines of the settlement. Endemic malaria is suggested to have been possible under such conditions. The malariogenic capacity is suggested, however, to have altered due to the environmental disturbances of this period; the deposition of alluvial soils would have significantly, although temporarily, altered the prevalence of local vectors, which, modern malaria studies have shown, can result in epidemic transmission.

***Early Helladic III/Lerna IV* (*2200/2150-2050/2000 cal. BC/ 4150/4000-4000/3950 cal. BP*)**

The succeeding period, EHIII, appears to have been one of environmental change. Faunal and archaeobotanical evidence would appear to reflect increasing aridity, which would concur with the palaeoclimatic data outlined in chapter three. Flax, (L.) (*Linum usitatissiumum*), a moisture-loving crop, disappears from the floral assemblage, potentially suggesting a decrease in water availability (Hansen 1988). Faunal assemblages from Lerna indicate a contemporary dramatic change in avian species, which appears to reflect an alteration in the local environment (Gejvall 1969). The EHII and early EHIII assemblages were composed of

grallatorial species (swimming and wading birds) such as *Phalacrocorax* (Brisson., 1760) (cormorant), *Ardeidae* (Leach., 1820) (heron), *Anatidae* spp. (ducks), and *Cygnus cygnus* (L., 1758) (whooper swan); these were abruptly replaced in EHIII by dry land species, such as *Alectoris graeca* (Meisner., 1804) (rock partridge), *Otis tarda* (L., 1758) (great bustard) and *Colombidae* (Illiger., 1811) (pigeon). These latter species are all suggested to have been newcomers to the faunal assemblage, indicating a definite change to the assemblage, and therefore to the immediate environment surrounding Lerna. Gejvall (1969) suggests that this trend is "typical for a biotope which changes from humid conditions with high level ground water [...] to drier [conditions] with greatly lowered ground water" (Gejvall 1969: 55). This alteration could have been initiated by climatic changes, the alluviation event of EHII, or anthropogenic activities such as extensive cultivation, as intensive agriculture has been known to alter the prevalence of local species in such a manner (Gejvall 1969).

The decline in water availability, whatever the cause, would have had equally significant effects on the malarial capacity of the plain; however, it must be noted that the reduction was not ubiquitous across the region. Coastal waters, swampland and Lake Lerna would have persisted and the discovery of several remains of *Lutra lutra* (L., 1758) (otter) amongst the faunal assemblage would also indicate that perennial streams persisted in the locality (Gejvall 1969). Areas such as these could well have become focal breeding grounds within a generally arid region, increasing the risk of infection considerably for those who lived in close proximity. Many vector species, such as *A. superpictus* and *A. sacharovi* favour dried up river beds, small pools and puddles as breeding grounds; reductions in water volume can therefore lead to an increase in this species (Bouma 1994a,b; Leishout 2004). *A. superpictus,* being particularly tolerant of aridity and dehydration, may have been able to withstand the changes and therefore have become a more prevalent species (Sabatinelli 2002). *A. plumbeus* is also noted to be particularly tolerant to drought as the larvae of tree hole breeders tend to be

protected from evaporation within the deep tree holes; studies have noted higher frequencies of such vectors when drought conditions are so severe that other species disappear (Howard *et al.* 1917).

Lower humidity levels for this period (2200-2000 cal. BC/ 4150-3950 cal. BP)[104], as indicated by palaeoclimatic studies (see chapter three), could have tempered the malariogenic capacity by reducing vector life spans; although the minimum humidity level of c. 60% in coastal locations in Southern Greece during modern history may suggest that the area was less affected by the event than inland regions (Gavrielides 1976 cited in Hansen 1991). The higher temperatures of this period would, however, have facilitated quicker development of both parasites and vectors; these climatic conditions, combined with the reduced water availability across the plain, are suggested to have created a high malariogenic capacity in intense, localised foci across the Argive plain.

Geoarchaeological studies of the Argive plain indicate that the environment appears to have remained stable throughout the EHIII period (Hansen 1988; Jahns 1993; Zangger 1993; 1994). Agriculture persisted, seemingly on a similar scale to that of EHII, however, animal husbandry increased in volume, with higher volumes of cattle and caprine herds, while equine species are noted for the first time (Gejvall 1969). The economy became increasingly centred on meat production, as evidenced by the proportion of young animals which were slaughtered (Gejvall 1969). Wild fauna decreased in importance in the diet; while Gejvall (1969) noted *Ursus arctos* (L., 1758) (brown bear), *Martes foina* (Erxl., 1777) (beech marten), *Lynx lynx* (L., 1758) (lynx), badger, otter, roe deer and hare among the assemblage, the frequency of wild game reduced from 22% in EHII to a mere 7% in EHIII. The locals may therefore have spent less time hunting wild animals from along the stream banks and

[104] 3777±13 ^{14}C yr BP – 3622±14 ^{14}C yr BP (Reimer *et al.* 2004)

collecting molluscs from brackish waters, but are suggested to have been exposed to other areas of malariogenic capacity through the increasing emphasis on herding and shepherding livestock. The shift in economic behaviour towards animal husbandry, particularly towards cattle herds which are favoured by many zoophilic species (Lividas *et al.* 1941), would suggest that infection rates may well have been mitigated amongst the late EH populations of Lerna (Lividas *et al.* 1941); however, the debate over the efficiency of zooprophylaxis renders this conclusion highly theoretical (Bøgh *et al.* 2002; Saul 2003; Kileen *et al.* 2004)

The settlement of Lerna altered significantly during this period as the site was rebuilt without fortifications or monumental buildings, signifying a change from a "palatial and military establishment [...] to a relatively simple [...] town" (Caskey 1986: 20) perhaps "not more than a small village" (Caskey 1960: 294). The reduced importance of Lerna during the EHIII period is reflected in other sites across the Peloponnese; following the widespread destructions of EHII, occupation density was notably reduced (Forsén 1992; Wright 2004). Surveys across Berbati-Limnes, Nemea and the Argolis indicate a sharp depopulation trend; however, the number of settlements gradually increased during the mid- Middle Helladic period (Wells *et al.* 1990; Jameson *et al.* 1994; Cherry *et al.* 2002). The widespread discontinuity in settlement patterns has traditionally been linked to invasion and migrations, although environmental and climatic causes, namely drought conditions, have more recently been proposed (Caskey 1960; Zangger 1992; Manning 1997). Regardless of the cause, the population densities, and therefore the potential host group, would undoubtedly have been reduced between EHII and EHIII; archaeological data would indicate that the occupation of the major sites of the Argive plain continued, albeit at a reduced density, throughout the EHIII period (Caskey 1968; Forsén 1992; Wright 2004).

The transition at Lerna to a “simple [...] town” (Caskey 1986: 20) is reflected in significant cultural changes; the introduction of apsidal houses, new material culture and perhaps the occurrence of the first *Equidea* (L.,1758) (ass) have been interpreted as potential evidence of an invading population, possibly from Asia Minor (Caskey 1960; 1986; Gejvall 1969; Weingarten 1997). This interpretation of the transition at Lerna has, however, been the subject of much scholarly debate (c.f. Rutter 1993); evidence for apsidal houses at Tiryns and Epidauros during the EHII period suggests that these architectural influences and foreign ‘invaders’ may have in fact been local populations occupying the site after the destructions of EHII (Forsén 2010). These, more local population movements, could still potentially have increased vulnerability to infection for both the autochthonous groups and the ‘invaders’, through the introduction of new strains or clones of the disease.

Wherever the inspiration for the architectural changes recorded at Lerna IV originated, the transformations were marked and are suggested to have altered the malariogenic capacity of the houses. The structures became apsidal or oblong in shape and were generally composed of two or three rooms, the larger containing a hearth. Construction materials appear less varied than those of Lerna III; no roofing materials have been recorded. Stone, crude brick and clay were the predominant materials for the walls; stone was frequently used as a socle for the walls, generally measuring less than a metre, on which the bricks were placed (Caskey 1954; 1960). Caskey (1960) notes, however, that these houses were largely less well constructed than those of EHII/Lerna III. Stone and crude brick are suggested to offer more protection than simple mud brick walls, however cracks in these or in the clay which was used to cover the superstructure (Caskey 1954) would provide similarly suitable niches for the endophilic vectors. The poorer construction quality of the houses would have increased exposure to nocturnal biting (Ye *et al.* 2006; Kirby *et al.* 2008).

Archaeological data indicate that water provisions within the urban environment may have been extended during this period, increasing potential *Anopheline* breeding grounds; *bothroi*, although used since the Late Neolithic, became particularly common along the narrow streets of Lerna. These small pits are suggested to have been originally built for storage away from the sunlight but eventually became rubbish pits, filled with bones, pot sherds and general waste material (Caskey 1960). These would be used by any urban-adapted vectors to their advantage; cool storage areas would attract mosquitoes seeking to rest from the heat of the day, while the rubbish pits, if open to pooling water, would create pools of high organic content. These create ideal breeding grounds for vectors, particularly *A. sacharovi, A. superpictus, A. atroparvus, A. claviger* and *A. plumbeus*, and provide particularly safe environments for larvae (Blacklock *et al.* 1920b; Aitkin 1954; Mitchell 2008). The *bothroi*, along with the wells, nearby lake and coastal marshes would suggest a potentially high exposure to malaria vectors within the urban setting.

The malariogenic capacity of the region during the EHIII period therefore appears to have been reduced. Firstly, the decline in population density following the destructions of EHII, both at Lerna and across the Peloponnese, may be suggested to have reduced the potential host group. Secondly, and perhaps most significantly, the well-noted global drought of 2200-2000 cal. BC/ 4150-3950 cal. BP[105] (see chapter three) would have affected the population density of the *Anopheline* vectors. The decreased humidity levels, coupled with the decrease in water availability, are suggested to have resulted in a reduction in the life span and breeding grounds of *Anopheline* vectors (Bruce-Chwatt 1980; Rohling *et al.* 2002). However, drought tolerant vectors, and those that favour transitory water bodies, would theoretically have become increasingly prevalent due to such hydrological changes. The evidence would

[105] 3777±13 ^{14}C yr BP – 3622 ±14 ^{14}C yr BP (Reimer *et al.* 2004)

therefore suggest that malaria was restricted to certain foci across the plain, most particularly to the anthropogenically altered landscapes. Combined with the elevated temperature, transmission may be suggested to have become more intense during this period.

***Middle Helladic/Lerna V* (*2050/2000-1680 cal. BC/4000/3950-3630 cal. BP*)**

The Middle Helladic is the only period of the Bronze Age for which there is a comprehensive skeletal assemblage at Lerna (see chapter one). Angel (1971) hypothesised, based on this data, that malaria was highly endemic during this period and, by extension, that the malariogenic capacity of the climate and landscape was considerable. As noted in chapter three, the general climatic trend over the Aegean was one of increasing aridity following the termination of the Holocene Humid Period (Rohling *et al.* 2002; Geraga *et al.* 2005); a trend which is suggested, based on modern malarial studies, to have reduced the malariogenic capacity. If Angel's (1971) theory is to be considered accurate, the malariogenic capacity of the landscape of Lerna would be expected to have been exceptionally high.

There is little evidence for any change in the environment of the Argive plain during the MH period. Geoarchaeological studies indicate that the landscape largely remained stable during this period; the coastline of the Argive Plain continued to regress, although this appears to have been an extremely gradual process. Pollen data indicate that anthropogenic alterations to the local environment were sustained from the previous periods (Zangger 1991; 1993; Jahns 1993); however animal husbandry altered significantly, as new domesticates appeared in the faunal assemblage. Wild cattle disappeared in favour of a domesticated strain, domesticated fowl were introduced and *Equus caballus* (L., 1758) (horse), as opposed to the ass, appeared for the first time (Gejvall 1969). Farming practices, deforestation and cultivation evidently persisted during the MH, which would undoubtedly have continued to create potential vector foci within these anthropogenic landscapes.

The early MH phases were characterised by small simple settlements; population densities remained low across southern Greece following the depopulation of EHII/EHIII, although occupation of the major sites across the Argive plain continued on a reduced scale (Bintliff 1977; Voutsaki 2010). Dickinson (1982; 1994) proposes that these societies were underdeveloped, lacking the economic and social complexity of EHII; Middle Helladic II-III were, however, periods of social, economic and cultural change. Surveys indicate more intensive land use and a gradual process of resettlement (Wright 2004). Argos rose to prominence during this period and quickly became a significant cultural centre, while settlement expansions (at Tiryns, Mycenae and Asine, for example) indicate increasing activity and the repopulation of the Argive plain and southern Greece (Wright 2004; Voutsaki 2010). By MHIII, sites across mainland Greece, and specifically the Argive plain, expand in size and begin to display increasing social, cultural and economic complexity that marks what Renfrew (1972) has termed "the emergence of civilisation". Displays of wealth, cultural advancements and expanding contacts, both foreign and local, would indicate an increasing host group (discussed further below).

Lerna remained a small but thriving settlement during the MH phase, although never regaining the prominence of EHII (Wiencke 1998). The construction and plan of the site show very little evidence of alteration from EHIII; the houses continued to be constructed in a similar style, shape, in the same materials and along the same town plan as during the previous period (figure 6.7). The design of the buildings, however, increased in complexity, as courtyards and storage rooms become attached to the apsidal houses. This may have altered the favourability of the dwellings for endophilic vectors; the cooler storage rooms would attract the resting vectors during the heat, drawing them away from the occupied rooms of the apsidal house. There is some evidence of fire destruction within the settlement

towards the later Middle Helladic period; these are however suggested to represent individual incidents rather than destruction phases (Caskey 1997). Effects on malarial patterns would therefore be minimal.

It is concluded that the MH period appears to have been as conducive to malarial transmission as the latter years of EHIII. The arid conditions (see chapter three) are likely to have limited infection by reducing the lifespan of the vectors; however the higher temperatures would suggest rapid sporogonic cycles and extended transmission seasons, suggesting a potential for intense, seasonal transmission. The environmental conditions of the plain appear to have remained stable; although the increase anthropogenic activity may have augmented primary *Anopheline* habitats.

***Late Helladic Period/ Lerna V- VII* (1680-1200/ 1180 cal. BC/ 3630-3150/3130 cal. BP)**

The Late Helladic was a period of climatic and environmental instability; the repeated climatic oscillations noted in the general climatic trends of the Aegean (chapter three) do not, however, appear to have left a lasting mark on the local vegetation or fauna. Environmental reconstructions from the pollen cores at Lake Lerna and geomorphological studies indicate that the variety and volume of water bodies within the plain persisted and, combined with the varying altitudes and areas of open landscape, could have continued to support vector population in small loci across the plain (Jahns 1993; Zangger 1993; 1994). It is suggested that the extreme diversity of the topography, particularly the rich diversity of water bodies, may well have protected the vectors from the increasing aridity after c. 1380 BC (3345 cal. BP)[106] (Rohling *et al.* 2002).

[106] Commonly dated in marine and pollen cores to a mean of 3100 ^{14}C yr BP (Reimer *et al.* 2004)

The occupation of Lerna during LHI coincided with the catastrophic volcanic eruption of Thera in c. 1627-1600 cal. BC (3687-3580 cal. BP)[107] and the potential effects of this event on the malariogenic capacity of the Argive Plain are worth considering (Manning 2006; Freidrich 2006). The scale of the eruption, suggested to be VEI 6-7, has led scholars to propose that both the climate and environment of the Aegean was heavily influenced by this event; global and local proxy data (discussed in chapter three) appear to reflect contemporary climatic anomalies as temperatures and humidity levels sharply declined (La Marche *et al.* 1984; Baillie *et al.* 1988; Geraga *et al.* 2000; Grudd *et al.* 2000; Rohling *et al.* 2002; Siklosy *et al.* 2009). Environmental changes are, however, not as evident; the data indicate that the Argive Plain would not have been directly affected by the eruption as Eastwood *et al.* (2002) suggest a northeast to southwest distribution of ash fall and tsunami debris and Dominey-Howes (2004) suggests a southwesterly to westerly direction for tsunamis. While pumice and ash deposits have been found across Crete (McCoy *et al.* 2000; Bruins *et al.* 2008), there is limited evidence for the effects of the eruption upon the mainland; Theran pumice has been found at Nichoria in the Peloponnese and ash deposits have been identified in Lake Trikhonis, although the identification of the latter is unverified (Rapp *et al.* 1973; Bottema 1982).

It is suggested that many of the effects of the eruption would not necessarily be evident in the archaeological record. The mainland was in such close proximity to the eruption that some repercussions must have been felt; the eruption of Tambora in 1815, another VEI 7 eruption, resulted in shock waves which were felt at nearly 1000 km distance, causing considerable structural damage to houses (Oppenheimer 2003). Mainland Greece, being in far greater proximity to the epicentre of the eruption, is therefore likely to have at least suffered ground

[107] Four dates of 3383±11, 3372±12; 3349±12 and 3331±10 ^{14}C yr BP were produced (Freidrich *et al.* 2006).

tremors. There is no evidence for severe structural damage (Caskey 1960; 1968), however, it is suggested that minor damage, such as cracked walls or streets would not necessarily be noted in the archaeological record. Such alterations, although minor, would modify malaria breeding grounds and perhaps the accessibility of the dwellings to the vector species. This region of Greece is, and is suggested to have always been, highly susceptible to earthquakes due to repeated actions between the Eurasia and Aegean Sea plate (Nur *et al.* 2000; Monaco *et al.* 2004); such minor disturbances on the mainland may therefore have been a frequent event.

It is, furthermore, worth considering the potential repercussions on malariogenic patterns, as many effects of volcanic eruptions would remain invisible within the proxy data. A comparison with more recent eruptions of a similar scale, such as Mt St Helens (1980) and Tambora (1815), would indicate that dust clouds, acid rain, dry fogs, erratic or extreme weather events and abrupt summer cooling are all possible consequences (Cook *et al.* 1981; Oppenheimer 2003). These would all alter the malariogenic capacity of the climate and environment and, however brief the oscillation, the mosquito populations; infection rates would therefore fluctuate. Other consequences would be more severe; acid rain, for example, would dramatically alter the aquatic ecosystems, killing both larvae and eggs and rendering the water body unsuitable for oviposition. Even very light ash fall would have particularly severe consequences on mosquito populations; the eruption of Mt St Helens demonstrated that insect populations were the most adversely affected of all organic systems, as ash particles engulfed the insects rending them incapable of movement or flight, most dying within hours (Cook *et al.* 1981). Soils and aquatic ecosystems can also be damaged by ash fall; even a thin covering of ash can reduce soil permeability and temperatures, while water bodies can become clogged or even toxic, depending on the chemical composition of the tephra (Cook *et al.* 1981; Driessen 2002). This would naturally reduce the malariogenic

capacity of the local environment by limiting mosquito breeding grounds. The effects of this volcanic eruption, although potentially highly significant, will not be dwelt on as there is no evidence for any such perturbations at Lerna. It is, however, suggested that climatic and environmental changes are likely to have occurred and even mild alterations would, it is suggested, have altered the malariogenic capacity.

Exposure to the potentially malarious habitats would also have increased during the Late Helladic period. Although Lerna had decreased in importance and the population is suggested to have decreased (Wiencke 1998), the number of sites within Argolidocorinthia gradually increased as did the prosperity of the region (figure 6.8). Surveys indicate that 27 settlements were situated across the Argive plain by LHIIIB; the citadels of Argos, Tiryns and Mycenae expanded in size, the latter two sites covering as much as 35-50 hectares, while towns such as Midea, Asine and Nauplion were over 1.5 hectares (Wright 2004). The resulting pressure on local resources would therefore suggest increasingly intensive land exploitation (Dickinson 1982; Hansen 1988; Wright 2004; Butzer 2005) which would augment the malariogenic capacity for most of the *Anopheles* vectors in question (Kuhn 2002), potentially permitting greater vector density.

Hansen (1988) reports that breadwheat appears at Tiryns, suggesting that crop rotation was employed, again indicating increasing emphasis on agriculture and labour intensive work in areas of high malariogenic capacity. Although there is no evidence for similar techniques at Lerna (Hansen 1988), the proximity between these sites would suggest that such advancements in agriculture would have been shared. The faunal and floral remains reflect this agricultural emphasis; Gejvall (1969) notes a striking increase in the number of

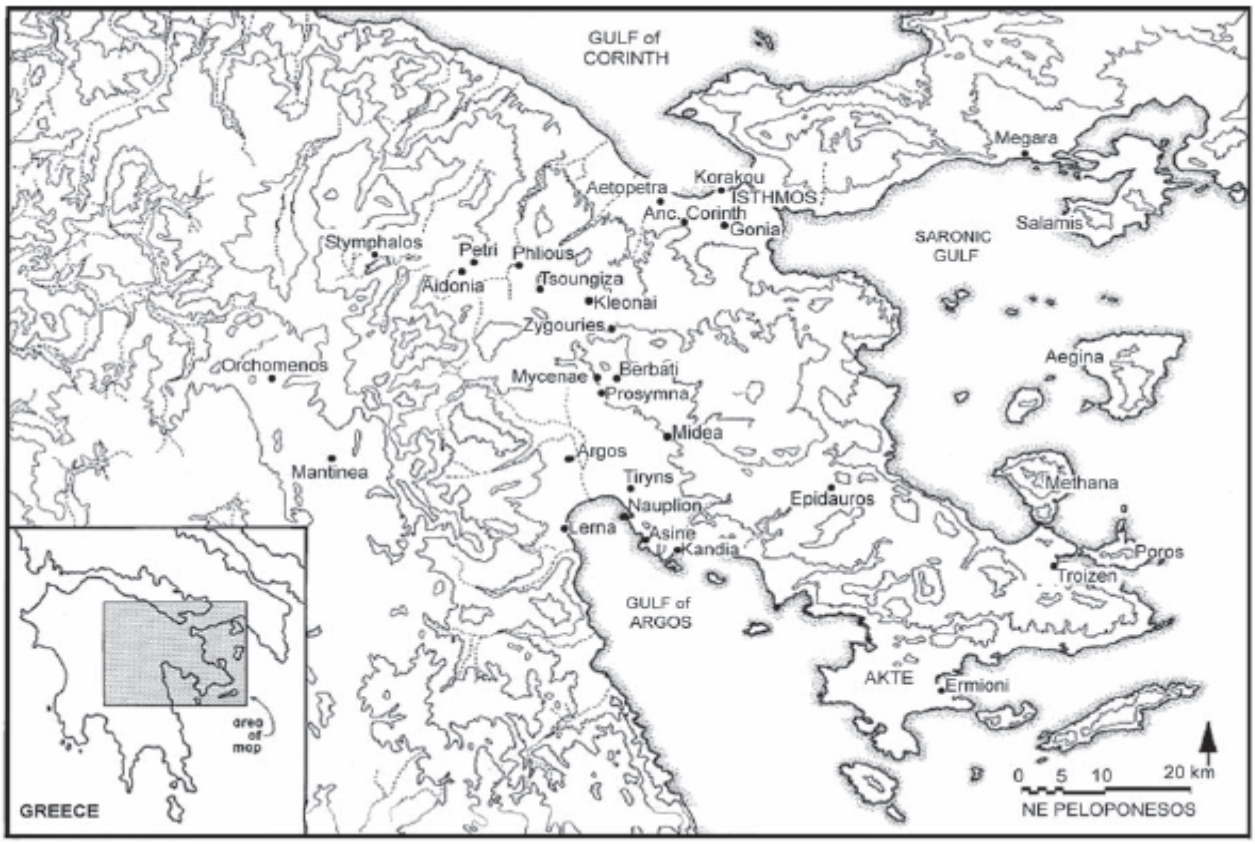


Fig. 6.8. Map of the Northern Peloponnese showing the main Bronze Age sites mentioned in the text (*After* Wright 2004: fig. 9.2: pg. 116)

domesticated species in the faunal record. Wild resources become almost insignificant within the assemblage, indicating an economy almost entirely based on meat production (Gejvall 1969: 59). It is again likely that the growing size of these herds would have increased grazing pressure; the late Helladic populations, therefore, spent less time hunting wild animals from along the stream banks but would, it is suggested, have exposed themselves to other areas of high malariogenic capacity.

Increased exploitation of the landscape during LHIIIA/B is well demonstrated by the development of an extensive and well-constructed road system that connected the large settlements across the Argive plain and north-east Peloponnese (figure 6.9). Jansen (2002) argues that the road systems were intra-regional, however Castelden (2005) argues for an inter-regional system, suggesting that the road system from Mycenae would have connected

to Corinth and the Isthmus and beyond. The increased facility for travel between the settlements and citadels across the region, particularly evident through the discovery of wheel ruts at the northern postern gate at Mycenae (Jansen 2002) combined with the augmented and nucleated populations, would indicate a larger host group for the *Plasmodiae* and an increased risk of transmission.

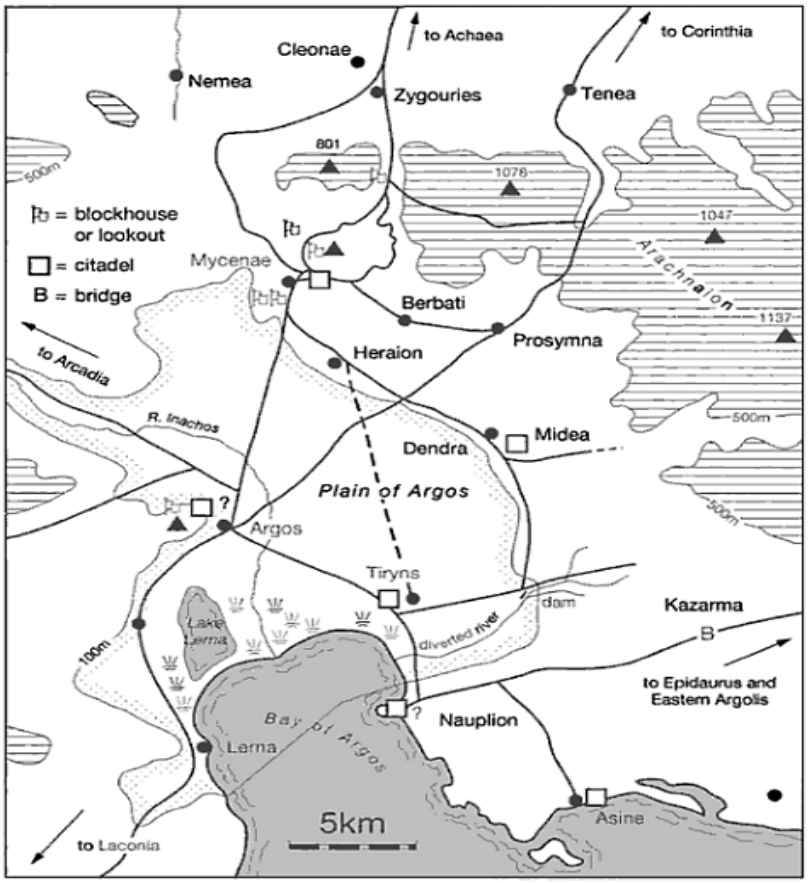


Fig. 6.9. Map of the Late Helladic road systems. Circles represent settlements, squares represent citadels; solid black lines are roads (*After* Castleden 2005: fig 2.8: pg. 36).

Modern malarial studies have repeatedly linked population movements with an increased vulnerability to malaria infection; increased mobility, through seasonal labour, trade or local exchanges, not only enhances transmission but can also introduce new *Plasmodiae* strains or

clones (Prothero 1977; Martens *et al.* 2000). Road construction can also lead to an intensification of land use as previously inaccessible areas become viable for anthropogenic use; this can result in the geographical expansion of the vector populations as new habitats are created (Patz 2000). Furthermore, the scale of the road construction indicates that significant changes to the local environment would have taken place, altering the existing ecology of the area and, by extension, the malariogenic capacity; as noted in chapter two, engineering and construction projects such as these can alter the relative densities of vector species, potentially affecting the incidence of malaria (Patz 2000; Yasuoka *et al.* 2007). The creation of the Late Helladic roads, which were cut and terraced into the hillsides (Jansen 2002), would have involved significant alteration to the existing landscape, including land clearance, the removal of top soil and digging of pits for foundations and embankments. Modern malaria studies indicate that such projects can drastically alter the microclimate, the permeability of the soils and can disrupt natural drainage systems, leading to increased volumes of surface water, and potentially, an increased incidence of malaria (Abisudjak *et al.* 1989; Vittor *et al.* 2006).

The settlement of Lerna showed some significant changes during the LH period, which may have supported the success of the vector populations throughout the increasingly erratic climatic and environmental conditions of the Late Helladic period. Most notably, the living conditions improved considerably; multiple rooms were added and archaeological data indicate the development of inbuilt drains (although this was only identified within one single house) (Caskey 1954; *et al.* 1997). The technological sophistication of the drainage systems was not likely to have been as advanced as those of the palaces of Middle Minoan Crete; these important sites were equipped with sophisticated plumbing systems which drained waste and storm water into subterranean sewage systems. Drains at Knossos were specifically designed to prevent pooling within the streets or along the uncovered stairways (Hutchinson

1950; Mays *et al.* 2007) which would have minimised breeding grounds within the settlement. Drainage systems of the mainland, or on smaller, rural or less important sites within Crete, were considerably more basic; drains at Tiryns, Mycenae and Pylos, for example, were simple ditches which were covered and lined with slabs (Blegen *et al.* 1961; Iakovidis 1983). A proportion of waste water would have in all likelihood been swept out onto the narrow streets where it would accumulate in pools; larvae would have been able to thrive in the water within the drains, in any developing pools surrounding the drain and at the outflow, creating viable breeding grounds and a high population density within the confines of the site. A great advantage of such breeding grounds for the vectors would be the lack of, or rarity of, predator species, such as fish, bats and birds, which would either be unable to exist in such locations, or reluctant to, due to the proximity to humans. The inbuilt drain at Lerna, although an isolated example within the site, would therefore indicate a potentially high malariogenic capacity within the settlement, placing malaria vectors in extremely close proximity to the inhabitants of Lerna.

There is unfortunately, little evidence for the construction of the houses in the latter part of the LH period as much evidence has been lost due to erosion and human activity. Wiencke (1998) notes however, that only a seventh of the mound, from which the Late Helladic evidence was discovered, has been excavated. Excavations suggest that the population of LHIIIA1 was small, as finds dating to this period are rare; this may be due, however, to a loss of evidence rather than a true reflection of Lerna (Wiencke 1998). As the Late Helladic period continued, the population is assumed to have increased, as the town continued to be modified on a fairly large scale. Wiencke (1998) suggests that infilling, dating to this period, was undertaken in order to correct the unevenness of the ground, perhaps in order to accommodate the expanding population. The lack of substantial evidence surrounding these buildings, however, precludes any interpretation of the layout with regards to the accessibility

for malarial vectors. There is little to no evidence pertaining to the structure of Lerna following LHIIIB due to the destruction of evidence by later anthropogenic activity; however the data indicate that by the LHIIIB period Lerna had lost all importance and was no more than a small settlement. There is no subsequent evidence for occupation, suggesting that the site was abandoned in late LHIIIB (Wiencke 1998).

The gradual decline of Lerna as an important site during the LH period appears to have roughly coincided with significant environmental, climatic and social instability across the Argive plain during Late Helladic IIIB. Palaeoclimatic data, outlined in chapter three, indicates that this period coincided with an intense drought; the increasing aridity is suggested to be visible in the archaeological record, as sites across the Greek mainland show a coeval change in the organisation of water sources. Cisterns were built into the Cyclopean walls at Tiryns, Mycenae and Athens, indicating a defensive element to water supplies; contemporary large-scale water systems were constructed in the form of a dam at Tiryns and extremely substantial irrigation canals were constructed along the Kopais basin (Dickinson 1994; Zangger 1994; Shelmerdine 1997). Moody (2005a) suggests that this focus on hydrological systems may reflect the increasing scarcity of water during the intense aridity of the thirteenth century BC. A reduction in water availability is not, however, reflected in the pollen, faunal or archaeological evidence from Lerna (Zangger 1993; 1994).

The increasing aridity coincided with multiple destruction events across the mainland; Tiryns, Mycenae, Midea and possibly Profitis Elias were all severely affected, although Lerna appears to have remained untouched by any of these events (Shelmerdine 1997; Wiencke 1998; Moody 2005a,b). The architectural damage to these sites has led some scholars to suggest that the destruction was due to earthquakes, as excavations indicate fire damage, distortion of the Cyclopean walls, the structural collapse of buildings and numerous skeletal

remains at Mycenae and Tiryns were discovered trapped beneath fallen masonry and debris (French 1996; Zangger 1991; 1994; Kilian 1996; Shelmerdine 1997). The Aegean is known to have been seismically active during this period (Van Andel *et al.* 1990a) and Nur *et al.* (2000) suggest that the area was subject to a series of related earthquakes which struck across the Aegean and Eastern Mediterranean.

Although these events do not appear to have directly affected Lerna, such upheaval occurring on the central Argive plain will have effected some changes to the local environment, which could have had serious repercussions on the established disease patterns. Seismic activity can alter the permeability of the rock and therefore alter the groundwater flow; recent studies have shown that such events often cause an "increase in stream, spring and seep discharge, some instances of springs going dry, or the appearance of new springs and a very few examples of decreases in spring discharge" (Sneed *et al.* 2003: 1; Gorokhovich 2005). It can also reduce the level of well water and alter the quality by, for example, introducing sea water, and can do so at great distances from the epicentre of the earthquake (Montgomery *et al.* 2003), all of which can take days, weeks or months to return to normal (Gorokhovich 2005). This would therefore suggest that the hydrological systems of the Argive Plain could have been drastically affected by these events, which would undoubtedly have the potential to affect the inhabitants of Lerna. It is impossible to determine if water levels were increased or decreased or the length of any such alterations; however such dramatic environmental events, occurring in conjunction with drought conditions, would certainly alter disease patterns.

It has long been argued that epidemics are closely associated with natural disasters such as earthquakes and volcanic eruptions; recent studies have, however, indicated such a link is in fact uncommon. Earthquakes and other such disturbances may cause *increased risk* of infection, as immunities weaken due to disruptions to water supplies, health care, shelter,

sanitation systems and food sources; epidemics are, however, rarely caused unless there is a significant factor with which to catalyse a rapid increase in the disease or disease vector (Floret *et al.* 2006; Watson *et al.* 2007). Such a catalyst appears to have been swiftly provided during LHIIIB; although the chronology of the events is uncertain, it has been suggested that the possible seismic event(s), coinciding with an increasingly erratic climate and increasing intensification of anthropogenic activities, may have acted as a catalyst for second phase of landscape instability along the Argive plain.

This late LHIIIB event was centred on Tiryns, where sediment analysis indicates that one, or maybe multiple, severe flooding events caused the lower town to be buried by up to 5 metres of alluvium (van Andel *et al.* 1990a,b; Zangger 1993; 1994). The flash flooding and severe alluviation deposits occurred to the north-east/east of Tiryns and Lerna was therefore, as before, not directly affected by the event; however, the metres of alluvial soils would severely disrupt the established ecosystems and habitats along the central plain. Breeding grounds across the plain would have altered dramatically; firstly, due to the excess of flood water which would increase the volume of surface water and form ideal breeding grounds. Secondly, and perhaps most significantly, the environmental changes attached to this event would alter the permeability of the soil; the infiltration rate of the saturated alluvial soils across the plain would be temporarily reduced, causing subsequent rainfall to gather within depressions. The erosion of topsoil from the uplands would interfere with the natural drainage systems in a more permanent manner, resulting in severely reduced absorption rates (Bruce-Chwatt 1980; Yasuoka *et al.* 2007).

It is suggested that the Tiryns dam and diversion channel was constructed in an attempt to prevent the reoccurrence of such a dramatic event (Van Andel *et al.* 1990a,b; Zangger 1993; 1994). This construct is broadly contemporary with the dams and canals within the Kopaic

basin in Boeotia (Shelmerdine 2001), and the construction of cisterns and water sources at Mycenae, Tiryns and Athens (Dickinson 1994), indicating advanced engineering ability and an increasing focus on hydrological systems. Contrary to Angel's (1971) suggestion that the development of water management systems would lessen the malariogenic capacity, modern studies have linked such systems to increased populations of *A. sacharovi*, *A. superpictus*, *A. maculipennis*, *A. plumbeus*, *A. claviger* and *A. atroparvus* (Lividas *et al.* 1941; Harmancioğlu *et al.* 2001). The dam is therefore suggested to have provided stable and consistent breeding grounds for the various sub-species of mosquito to thrive; permitting potentially dense mosquito populations to co-exist in extremely close quarters with the inhabitants of the Late Bronze Age towns and palaces.

Transmission may have been exacerbated further by population movements. The multiple environmental events occurring across the Argive plain at the transition between LHIIIB and LHIIIC may have contributed, along perhaps with socio-political unrest, to the devastation and abandonment of many sites including Lerna, Midea, Berbati and Katsingri (Zangger 1994; Drews 1995; Kilian 1996; Wiencke 1998; Butzer 2005). Mycenae and Tiryns were reoccupied and the latter in fact expanded in size, perhaps reflecting a nucleation following the environmental disasters. The final destructions across the plain, be it by fire, unrest or earthquake, combined with mass social upheaval and population redistribution would have further increased vulnerability to disease. Forced displacement of population groups due to war, unrest or disaster within malarious regions is considered to be "a precipitating cause of the most serious malaria problems" (Bloland *et al.* 2003: 3; WHO 2005). Overcrowding, disruption to sanitation systems, poor shelter facilities and lack of food result in impaired immune systems, and an increased vulnerability to infection; epidemic outbreaks are a distinct threat under such conditions (WHO 2005).

The Late Helladic period at Lerna therefore appears to have been one of great climatic, environmental and social upheaval. The reconstruction of these factors would suggest that the climatic fluctuations and the continuing alterations of the landscape would have resulted in increasingly unstable malaria patterns as the Late Helladic period progressed. The marked aridity of the Bronze Age climate (see chapter three), coupled with the continued deforestation, would have removed *A. plumbeus* as a potential vector; however the land clearance, increasing emphasis on farming and the hydrological constructions, both within and outside the settlement, would have increased the viability of the region for the primary vectors. It is suggested that the type of water bodies surrounding Lerna and within the site would result in a potential for high densities of *A. sacharovi, A. superpictus, A. maculipennis, A. atroparvus, A. claviger, A. melanoon* and *A. hyrcanus.*

The latter part of the period, particularly the last phase of occupation, would have undoubtedly witnessed particularly erratic transmission patterns. The fluctuating climate, punctuated by increasingly frequent phases of severe aridity and extreme weather events, such as the flooding at Tiryns, would have resulted in highly irregular malaria patterns. These would have been exacerbated by the repeated environmental disasters which struck the area. The seismic activity, severe phase of landscape instability, subsequent hydrological changes and intensive land clearance would have repeatedly altered the ecosystems and disturbed the vector habitats. It is suggested that the combination of these events would promote a fluctuating malariogenic capacity and, potentially, increasingly unstable malaria patterns.

Malaria and trade during the Early to Late Helladic period

The complexity of the relationship between malaria and trade, combined with the expansive and widespread trading networks of the Bronze Age Aegean, requires this subject to be considered within this separate section. Trade is particularly significant to disease patterns as intra-regional connections will expand host groups and potentially diffuse infectious diseases. Long distance travel will give rise to wide geographical expansions of the *Anopheles* mosquitoes, increasing the host reservoir and potentially causing epidemic outbreaks amongst non-immune or previously non-exposed population groups (McNeil 1979; Martens *et al.* 2000).

The location of Lerna was particularly advantageous for trade. The site lies at a point where the Argive Plain narrows between the sea and foothills; Lerna therefore had strategic influence over the Gulf of Argos and the overseas trade routes, as well as coastal routes to Arkadia and across the Argive Plain (Wiencke 2000). Contact with the Cycladic islands is evident from the Middle Neolithic period as Lerna sourced obsidian from Melos, an exchange which continued throughout the Bronze Age (Caskey 1968; Runnels 1985). The Early Helladic period saw a rapid expansion of local trade routes, as the Cycladic islands played a central role in distributing ceramics, metal and obsidian goods throughout the Aegean, characterising what Renfrew (1972) refers to as the international spirit of the Early Bronze Age Aegean. The development of this network would have exposed the populations of the Aegean to a far wider host group than previously possible; contact with distant regions could potentially prompt a geographical expansion of local vector species and potentially introduce new strains of the disease.

Evidence suggests that Lerna would have become particularly exposed to other population groups as the site became a trading centre of some importance during the late EHII. Caskey

(1957; 1960) and Weingarten (1997) have argued that the House of Tiles formed the hub of a highly organised trade network; the style of seals, houses and the fortifications, suggesting strong Anatolian links. It has been argued, however, that the Anatolian influence at Lerna was not the result of direct contact; Şahoğlu (2005) suggests that the lack of Anatolian ceramics within the Peloponnese during this period indicates that the cultural and architectural influences from the Near East were the result of indirect contact, perhaps through other trading sites such as Aegina-Kolonna. Foreign wares were certainly penetrating into the Aegean during this period, as Crete traded with Egypt, Anatolia and the Near East, indicating that the potential host group within the Mediterranean was increasing and the geographical spread of diseases was becoming increasingly probable (McNeil 1979; Krzyszkowska 1988; Dickinson 1994). Foreign diseases or vectors may not, therefore, have been arriving directly from North Africa or the Near East to Lerna's shores; nonetheless, even indirect contact with other civilisations and population groups would have aided the diffusion of diseases and increased the vulnerability to disease.

The settlement destructions at the termination of EHII and the resulting depopulation of the southern Argolid during EHIII may be suggested to have led to an economic downturn; archaeological evidence indicate extremely minimal trade links at Lerna during this period (Caskey 1968). Local trade networks expanded further during the Middle Helladic, encompassing the Argolid, Attica, the islands in the Saronic Gulf, Boeotia, Euboea and the Cycladic islands with Lerna in particular contact with Kythera (Zerner 1993; Dickinson 1994). Foreign contact is suggested to have remained indirect, as the very few artefacts indicating contact with Egypt from the Argive plain are unsubstantiated (Lambrou-Phillipson 1990); Cretan links with the Near East and Egypt had, however, strengthened, suggesting that Crete may have acted as intermediary (Lambrou-Phillipson 1990; Cline 1994).

The wealth of the Shaft-Graves at Lerna indicate increasing prosperity of the site by the LHI, while the more exotic grave goods from the Shaft Graves at Mycenae, dating to the late Middle Helladic until (early) Late Helladic II, indicate a strong dependence on foreign goods as symbols of wealth and prestige (Graziadio 1991; Voutsaki 1995). Ivory, precious metals, amber and lapis lazuli are present, indicating contact with Egypt, Syrio-Palestine, Northern Europe, Cyprus and possibly Afghanistan; however, it is suggested that Crete continued to act as a main channel for the exchange of foreign goods during the early Late Helladic Period (Harding 1984; Krzyszkowska 1988; Graziadio 1991; Dickinson 1994).

It is proposed that direct trade routes emerged during the Late Helladic II/III (Mee 1978; Sherratt 1993); European amber appeared in large quantities in the Peloponnese (Harding *et al.* 1974) while Asiatic, Egyptian and Cypriot goods become increasingly prevalent across the Aegean (Lambrou-Phillipson 1990; Cline 1994). Lerna had, however, lost prominence within the Argive Plain by Late Helladic III (Wiencke 1998) and was no longer as active in trade affairs; Mycenae and Tiryns became prominent centres of manufacture and distribution until the end of the Bronze Age, both sites revealing large quantities of both foreign and Aegean products (Cline 1994). The archaeological evidence for trade within the Argive plain during this period is overwhelming; shipwrecks, artefacts and literary evidence from Linear B tablets suggest that the Mycenaeans were trading with most of the countries within the Mediterranean. Contact was firmly established within the local islands, with countries to the west, including Italy and Sardinia, and to the east including Mesopotamia, Anatolia, Cyprus, Syro-Palestine and Egypt (figure 6.10) (Mee 1978; Lambrou-Phillipson 1990; Cline 1994). Cline (1995) further presents artefactual, textual and cultural evidence for expatriate Mycenaeans working as mercenaries, merchants, ambassadors and artisans in the Levant, Mesopotamia, Anatolia and Egypt.

The development of foreign trade, especially within networks as extensive as those that had developed by the Late Helladic period, is suggested to have facilitated the movement of disease vectors enormously, permitting rapid and expansive geographical distributions. *P. falciparum* is known to have been active in Egypt by the Late Bronze Age (Nerlich *et al.* 2008; Hawass *et al.* 2010); the extensive trading contact between Egypt and the Aegean would therefore have undoubtedly resulted in the transfer of vectors, malaria strains and of other diseases.

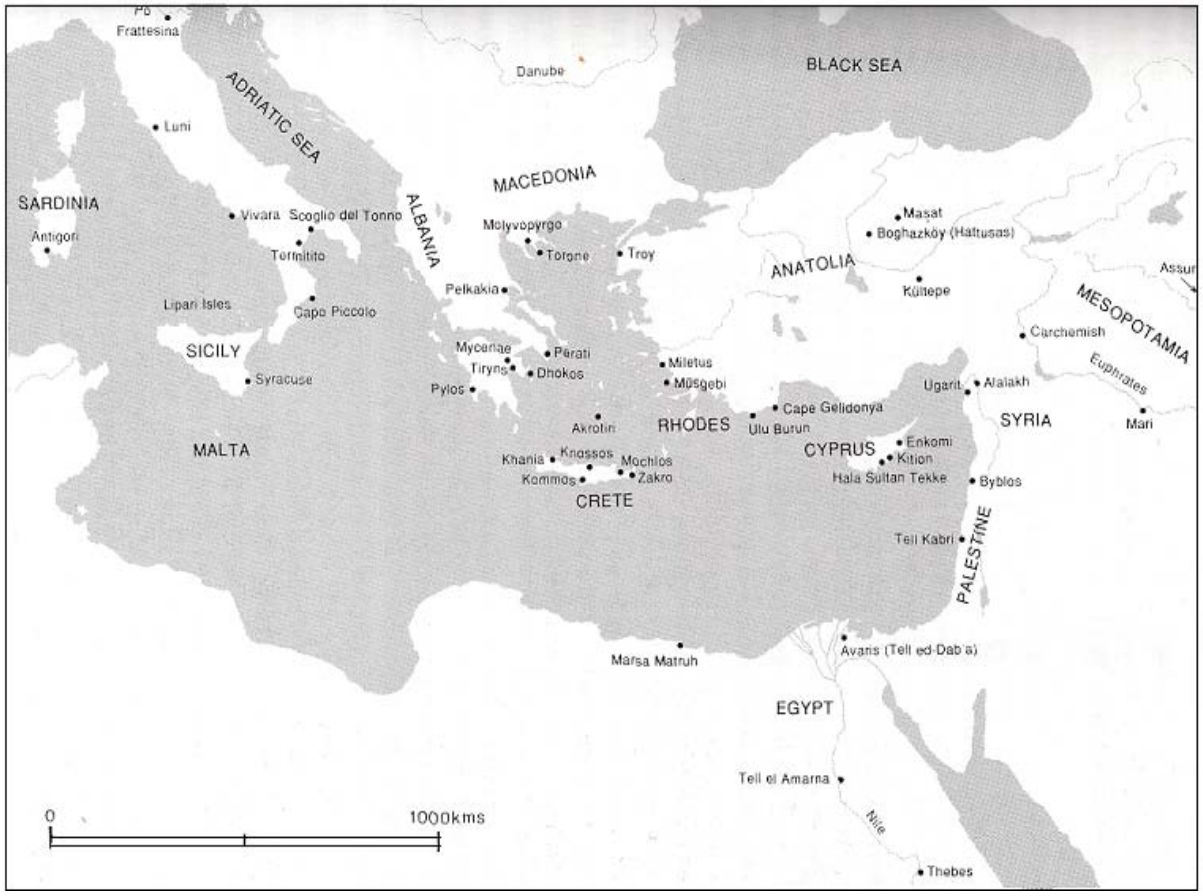


Fig. 6.10. Map showing the extent of overseas contact in the eastern Mediterranean and the Near East during the Late Helladic (*After* Dickinson 1994: fig. 7.1: pg. 235).

Studies have demonstrated that trading cargo vessels can result in frequent and dangerous migrations of foreign vectors and malaria parasites into previously unaffected areas; *Anopheles* larvae and adult vectors have shown to be highly tolerant, travelling considerable

distances under highly stressful and unfavourable conditions (Lounibos 2007). It would therefore appear comparatively simple for an infected foreign sailor or merchant to introduce a new strain of malaria into the Argive Plain or for an infected *Anopheles* mosquito or vector larvae to survive a crossing of the Mediterranean on a Bronze Age cargo ship.

Contemporary shipwrecks from the Mediterranean indicate that trading vessels had large carrying capacities with which to facilitate the migration of these vectors; the Uluburun shipwreck is estimated to have had a 20 tonne capacity, which contained pithoi, amphorae and other containers (Pulak 1998). Both mice and snails have been identified as stowaways amidst the remains of this wreck (Welter-Schultes 2008; Cucchi 2008) and it is suggested that *Anopheles* vectors may also have been transported by resting amongst the cargo; pools of water, collected within man-made containers would support larvae, while adult vectors could become trapped within pithoi or other cargo goods.

Infected vectors are obviously the main threat due to the potential of virulent epidemics, when disease is introduced to a previously unexposed area (Bruce-Chwatt 1980; Nájera *et al.* 2005). A particular danger is derived, however, from the genetic variability of the malaria *Plasmodiae*; while the numerous genetic immunities of the Mediterranean would provide some protection against foreign strains of malaria, an individual with acquired immunity to a local strain will not necessarily be protected from the same strain from another region (Babiker *et al.* 1997; Freitas-Junior *et al.* 2000). The Egyptian strain of *P. falciparum*, or of *P. vivax* or *P. malariae*, would, therefore, present a severe threat to local populations. It is concluded that trade routes would have increased the vulnerability of some populations to infection. The decline of Lerna as an important trading centre during the Later Helladic is not suggested to have reduced the potential vulnerability of the population to foreign pathogens, as Argos, Tiryns and particularly Mycenae remained significant centres of trade until the end of the period (Cline 1994).

The threat of disease expansion would, however, have come from both directions; as the population of Lerna could have been exposed to new diseases, vectors and malaria strains, so too could foreign traders have been exposed through contact with Greece. The suggested high malariogenic capacity of the climate and of the Argive Plain, combined with the seasonality of the trading season is suggested to have exposed the foreign traders to a risk of infection. Trading is suggested to have been prohibited between November and April by the wind systems and winter currents (Agouridis 1997); contact would therefore have coincided with the peaks in the malarial season. The evidence for *P. falciparum* in North Africa during the Early Bronze Age would suggest that these populations were exposed to the malaria parasites and had potentially developed immunities; however, the existence of *P. falciparum* or of genetic immunities in other regions of the eastern Mediterranean has not been proven for the Late Bronze Age period, either through DNA studies or literary sources. Traders from the western Mediterranean regions may therefore have been at greater risk (Sallares 2002; 2004).

The expanding trade routes of the Bronze Age Aegean are suggested to have resulted in significant changes to established malaria patterns. The increasing frequency of local and foreign contacts on the Argive Plain during the Bronze Age is suggested to have, firstly, resulted in increased vulnerability to disease, as other infections and diseases would have been imported to which the populations of the Argive Plain would have had no immunity. The subsequent weakening of the immune system would then render the individuals more susceptible to malaria infection. Secondly, the broadening trade network would have resulted in a geographical expansion of the malaria vectors as the ships or overland traffic may have unwittingly carried the vectors from region to region. Lastly, it is suggested that the regularity of contact with different cultural groups would have caused an immense increase in the host group; this would help boost infection rates and the prevalence of the disease. Epidemic transmission is suggested to have been a frequent occurrence, especially given the seasonality

of both the Bronze Age climate and the trading seasons. Trade is therefore suggested to have played an extremely important role in malaria during the Bronze Age; the Aegean, as a trading centre of some significance, would have been highly exposed to virulent disease patterns that multicultural contact can promote.

Discussion

A reconstruction of the local climate and of the natural and social environment of Bronze Age Lerna would therefore support Angel's (1971) theory. Angel (1971) indicated that malaria would have been endemic on the Argive Plain during the Middle Bronze Age although the prevalence was less than that of previous periods and declined throughout the Late Bronze Age (1971). This study would broadly support this contention; palaeoclimatic reconstructions of the Aegean during the Bronze Age would suggest a steady decline in malariogenic capacity for endemic transmission, as temperature and humidity levels repeatedly fluctuated within a general trend of increasing aridity. However, it is concluded here that the economic and social advancements of the Middle to Late Helladic period and the resulting anthropogenic environment would have maintained a high malariogenic capacity on the Argive Plain in spite of the climatic deterioration. This study would, therefore, contradict Angel's (1971) hypothesis of a declining capacity, but would rather indicate a potential transition from endemicity to increasingly unstable malarial patterns.

The Bronze Age would undoubtedly have been less conducive for endemic transmission than previous periods; although temperatures were relatively higher, the decreasing humidity levels after the termination of the HHP would suggest a far lower malariogenic capacity in comparison with the wetter conditions of the Neolithic. Environmentally, however, the region is suggested to have been highly viable for the *Anopheline* vectors; the variety of ecological niches, highland and lowlands, coastal and inland habitats, combined with the high volume of

surface water would have provided an abundance of habitats for the main *Anopheles* vectors to co-exist within a remarkably small region. The diversity of the landscape may have afforded some protection against the climatic changes which followed, permitting malaria to persist despite the increasing aridity.

It is suggested that the dramatic increase in aridity during EHII would have rapidly altered existing malaria transmission patterns. The extremely low humidity levels would shorten vector life span. An equally crucial factor, however, is the resulting reduction in water availability; this appears to have repeatedly occurred during the Bronze Age, most markedly during EHIII/MH and the LHIII period. While this reduction may have reduced breeding grounds for vectors favouring flowing water bodies, it would also encourage intense breeding foci to develop where water sources persisted, particularly in the vicinity of the marshland. Human health at Lerna may therefore have become particularly compromised, as the site lay in extreme proximity to the areas of marshland, Lake Lerna, springs and brackish waters and would have contained many viable breeding grounds within the settlement. This suggestion is contrary to Angel's (1971) hypothesis that drier periods led to the suppression of vector densities and therefore of infection rates and wetter periods promoted vector abundance, leading to increased infection rates and extended transmission seasons.

These changes would have been further exacerbated by social and economic development and increasing urbanisation, which may have maintained *Anopheline* densities when the climatic conditions were largely unfavourable. Anthropogenic alterations to the landscape such as deforestation, the introduction of ploughing, the adoption of large-scale agriculture and animal domestication would have altered the malariogenic capacity and, based on modern malariogenic studies, are suggested to have potentially increased the malariogenic capacity for the primary *Anopheline* vectors. The effect of such a change could be crucial to

infection rates; any event causing anthropophilic or endophilic vectors to increase in volume over zoophilic or exophilic vectors will naturally promote higher infection rates, assuming a constant parasitic burden.

The growing instability within the transmission patterns would have been exacerbated by the extreme weather events, episodes of landscape instability, environmental catastrophes and settlement destructions during the Late Helladic period. The repeated disturbances would strongly affect both human immunity and the density of vector populations, both of which can result in virulent epidemics. It is therefore proposed that by the end of the occupation of Lerna, epidemic or unstable infection patterns would have become increasingly common.

The expansion of social networks would also have contributed to erratic disease patterns, especially during the Middle and Late Helladic period, when both inter-regional and foreign contacts expanded and trade with Egypt, Anatolia, Syrio-Palestine and Cyprus became direct; 'foreign' strains of malaria, foreign vectors and other communicable disease may therefore have been transmitted directly. The multicultural societies of EH III and the Late MH to LH period is, therefore, highly likely to have harboured multiple malaria parasites.

A reconstruction of the climatic, environmental and social conditions surrounding Lerna therefore indicates a considerable malariogenic capacity which could have initially supported endemic malaria. The climatic capacity gradually declined as the Bronze Age progressed; however, the increasing social and economic complexity of this early urban society would have undoubtedly enhanced malarial survival. The reconstruction therefore indicates a transition to a different malaria pattern rather than a termination to malariogenic capacity. It is concluded that malaria could have placed a considerable burden on the inhabitants of Bronze Age Lerna.

Limitations of this study

The malariogenic capacity of an ancient landscape is extremely difficult to reconstruct, especially during archaeological phases for which textual records are absent, osteological records are few and the preservation of archaeological data is frequently poor. While palaeoclimatic and environmental reconstructions are considered viable methods for ascertaining the general malariogenic capacity, there are many limitations in the scale and scope of proxy data that preclude definitive conclusions from being drawn. As noted in chapter two, malaria is dependent upon micro-scale parameters, factors which are rarely evident in proxy or archaeological data; interpretations as to malariogenic capacity are, therefore, generalisations. Any reconstructions of disease patterns are tentatively made.

Caution is, furthermore, required when applying empirical evidence of malariogenic determinants to the past. The theory of uniformitarianism is limited in many regards in this topic; while it is assumed that the climatic and environmental tolerances and the lifecycles of the *Anopheline* vectors and malaria parasites have not altered, many important anthropogenic malarial determinants have changed significantly between the Mesolithic and the present day. This chronological range encompasses a period of considerable social and economic development, which would have irrevocably altered the relationship between man and mosquito. However, there are no direct parallels of such a social and economic evolution in modern societies and many malariogenic determinants cannot, therefore, be reconstructed. Direct correlations with modern malaria studies are therefore of restricted use when attempting to consider potential infection rates and are made with caution.

Although with considerable limitations, this thesis concludes that reconstructions of general climatic trends and environmental conditions are, however, sufficient to ascertain the overall malariogenic *capacity* of the various regions in question. While malaria *patterns* can rarely be

projected, it is possible to establish whether the general climatic and environmental conditions were viable for the *Anopheline* vectors and malarial *Plasmodiae* to have survived, and to determine the extent to which the prehistoric populations were exposed to such conditions.

Chapter 7: Conclusion

The palaeoclimatic and environmental reconstructions outlined within this thesis broadly concurs Angel's (1969a; 1971; 1972) hypothesis of a high malariogenic capacity between the Mesolithic and Late Bronze Age. The climatic and environmental data with which Angel supported his hypothesis is now considered erroneous in either accuracy, or in its application to the Mediterranean; however, the evidence considered within this thesis would support the underlying theory that both the climate and environment of these three sites were conducive for malarial transmission.

It is concluded that *P. falciparum* could not have been introduced into the Greek mainland prior to the Mesolithic, as the cold and arid conditions of the Younger Dryas would have undoubtedly precluded the strain from successfully completing development cycles. The climatic evidence would, therefore, support the theory that a genetic condition could not have developed amongst the local inhabitants by the Mesolithic Period. The suggested seasonality of the climate during the Younger Dryas may, however, have supported both *P. vivax* and *P. malariae*, which are more tolerant of colder conditions.

It is proposed that *P. falciparum* could have been successfully introduced into the Aegean after the climatic amelioration of the Lower Mesolithic. Conditions are suggested to have been more viable for malarial transmission than those of the 1930s; winter temperatures and precipitation levels exceeded the modern and were undoubtedly sufficiently high to promote rapid reproduction rates and sporogonic cycles, increased population densities, extended transmission seasons and increased biting behaviour. The argument concerning the exclusion of *P. falciparum* from the Aegean during this, and subsequent periods, due to unfavourable environmental conditions for the tropical *Anopheline* vectors is refuted. Firstly, as local

Mediterranean vectors, specifically *A. plumbeus, A. atroparvus* and *A. melanoon,* have now been shown to be receptive and efficient carriers of 'tropical' strains of *P. falciparum*. While transmission would undoubtedly have been enhanced by the presence of the tropical vectors, it may now be argued that the transmission of this strain in early periods would not have hinged upon the introduction date of these *Anopheline* vectors into the Aegean.

Secondly, environmental reconstructions of the three sites considered within this thesis do not support the theory that the Aegean was too densely forested to sustain the tropical vectors until the Hellenistic or Roman Period (Borza 1979; Bruce-Chwatt *et al.* 1980; de Zulueta 1994). The pollen records, archaeobotanical, geomorphological and faunal evidence would instead indicate a mosaic of vegetation types within highly varied topographical settings, indicating far less densely forested environments between the Mesolithic and Late Bronze Age than previously envisaged. The woodland cover of each site was undoubtedly more extensive than that of the modern period; it is suggested, however, that this may have limited, rather than precluded, the distribution of the 'tropical' vectors, while enhancing the capacity for the 'native' vectors of Greece, many of which favour woodland or shaded habitats. As some of the latter vectors of Greece are now known to be receptive and virulent carriers of this virulent strain, *P. falciparum* transmission is suggested to have been possible during these early periods.

Environmental reconstructions from Franchthi Cave would therefore support the contention of a considerable malariogenic capacity, indicating a diverse landscape which could, theoretically, have supported all the vectors found in Greece during modern history. Contrary to Angel's (1969a) theory, however, it is considered unlikely that malaria was highly endemic during the Mesolithic period. Despite the high malariogenic capacity of both the climate and local environment, the social and economic structure of the Mesolithic society is

suggested to have restricted human exposure to the *Anopheline* vector habitats. Endophilic and endophagic behaviour amongst the vectors would be seasonally limited during the Mesolithic due to the cold and damp nature of the cave, while the lack of evidence for anthropophilic influence on the landscape would equally suggest that exposure to infection would be restricted. The malariogenic capacity of the region would, however, indicate a capacity for all three *Plasmodiae*, and combined with the extensive exploitation of the surrounding resource bases, would suggest a sufficient exposure to vector habitats to support a low to moderate disease burden.

Endemic transmission is, however, considered highly plausible during the Neolithic Period, due to both favourable climatic and environmental conditions and marked changes in anthropogenic behaviour. The exceptionally elevated temperatures and precipitation levels of the Holocene Humid Period, coinciding with the adoption of increasingly complex economic and social activities, would suggest a significant increase in the malariogenic capacity of the regions in question. The creation of man-made microclimates and microenvironments would have been particularly instrumental in increasing the potential for human exposure to anthropophilic vectors. The reduced biodiversity of the landscapes, even when enacted on a small scale, would have increased primary vector breeding grounds and introduced a greater capacity for high vector densities. The concurrent development of early urban environments would have further favoured these *Anopheline* vectors, promoting endophagic behaviour, increased rates of reproduction and development, augmented lifespans, extended transmission seasons and, consequently, increased human exposure to the disease. As abundance and exposure are considered primary factors in malarial transmission, it is logical to suggest a higher malariogenic capacity during the Neolithic period.

The environmental capacity is, however, considered to have remained high for all *Anopheline* vectors, not just the primary; the early farmers were exposed to a wide variety of *Anopheline* habitats, from open land to dense forests, which is suggested to have enhanced the risk of transmission, promoting both sylvan and urban vectors. With the exception of the two hundred year climatic deterioration in c. 6250 cal. BC, which would have limited the malariogenic capacity, it is concluded that the Neolithic climate and environments of Franchthi Cave and Nea Nikomedeia were highly viable for endemic malarial transmission.

The termination of the HHP at the beginning of the Early Bronze Age and the increasingly arid and erratic climate of the Middle to Late Bronze Age would indicate a distinct transition to a lower malariogenic capacity. Climatic reconstructions would, therefore, concur with Angel's (1966; 1969b; 1971) theory of a decreasing malariogenic capacity, consequential decline in the frequencies of *Porotic hyperostosis* and, by extension, in genetic immunities during this period. It is concluded, however, contrary to Angel's (1971) theory, that the suppressive effects of this climatic deterioration on malarial transmission would have been mitigated by the increasing social and economic complexity of the Bronze Age society on the Argive Plain. Cultural and socio-economic advancements, manifested in greater population densities, an increased number of sites, complex urban planning, agricultural expansion, water management and the expansion of both local and foreign trade networks, would indicate a greater environmental capacity for malarial transmission than is evident for the previous archaeological periods discussed within this thesis. While some technological advancements, such as ploughing, may have reduced the prevalence of *Anopheline* breeding grounds, it is suggested that the expansion in anthropogenic influence and increasing sophistication of the urban environments would have intensified the malariogenic capacity of the Argive Plain, facilitating a higher abundance of anthropophilic vectors and a greater potential for transmission.

That *P. falciparum* was present within the Mediterranean during this period is confirmed by aDNA evidence from Egypt (Hawass *et al.* 2010), which indicates that the most virulent strain was undoubtedly extant within the Bronze Age trading regions; it is therefore concluded that both this, and the 'lesser' strains, were not only extent, but also highly active within the Aegean. Reconstructions of the malariogenic capacity of the Argive Plain during the Bronze Age therefore concur with Stravopodi *et al's* (2009) interpretation of the frequencies of *Porotic hyperostosis* and potential malarial transmission, which indicate an increase of the skeletal markers amongst Bronze Age skeletal assemblages, rather than Angel's (1971; 1972) interpretation of a declining malariogenic capacity.

The importance of this study lies within the severe implications of the disease burden, manifested both in malarial infection and in the symptoms associated with genetic and acquired immunities. The fevers, anaemia, malaria cachexia and the many physical and mental symptoms would have important consequences on day-to-day life and on the economic and social progress of these early societies. In hunter-gatherer societies, the incapacitation of individuals would severely threaten food procurement and would increase the risk of malnutrition. The threat of infection could furthermore have limited population movements and may, as a consequence, have influenced the diffusion of technological ideas and advancements. In later cultures, the potential for infection could compromise economic expansion, intra-regional or international relations, causing severe economic damage amongst these developing societies and compounding poverty. It is further suggested that demographics and productivity would be affected by the genetic immunity, β-thalassemia. The short lifespan of homozygotes would limit population growth, while mild to severe anaemia, in both heterozygotes and those with acquired immunity, would result in slower development times amongst children and lethargy amongst the general population. Cultural, economic and social progress may therefore have been compromised within these incipient

societies and the significance of these factors upon the Mesolithic to Bronze Age populations of mainland Greece cannot, therefore, be ignored.

It is reiterated that the search for *P. falciparum* should not obscure the significance of *P. vivax* and *P. malariae*. The mortality rates attached to these strains are not as substantial; however, the socioeconomic consequences are equally as pernicious as those of *P. falciparum*. The threat of relapses, which is specific to these strains, would indicate a repetitive and debilitating burden; coupled with malarial cachexia, congenital infection and the physical and mental complications that accompany *P. vivax* and *P. malariae* infections, it is concluded that the presence of these strains would be sufficient to impose a heavy disease burden, limiting the labouring and creative progress on these early societies. The climatic tolerances of these strains, and of the many *Anopheline* vectors that are receptive to them, would furthermore indicate a longer history of transmission within the Aegean than *P. falciparum*. Both *P. vivax* and *P. malariae* may, therefore, have already been well established within the Mediterranean by the Mesolithic period, and consequently have presented a greater threat to the hunter-gatherer populations than the more virulent strain. It is concluded that these strains presented an equal threat to the Neolithic to Bronze Age populations of mainland Greece as *P. falciparum*.

Many unanswered questions remain within this topic; while osteological studies now consider Angel's (1966; 1969a; 1971; 1972) interpretation of skeletal lesions to be plausible (although his statistics to be exaggerated in frequency), positive evidence for the existence of *P. falciparum*, or for *P. vivax* and *P. malariae*, can only be provided by aDNA evidence for *Plasmodial* infection within ancient human remains. As preservation problems preclude aDNA analysis from being applied to remains dating to these early societies in the Aegean region, correlations with evidence from adjacent countries are the only secure method of identifying the presence of malaria *Plasmodiae* within the Mediterranean region. In the

absence of such evidence, a consideration of the malariogenic capacity through palaeoclimatic and palaeoenvironmental studies, although providing only circumstantial evidence, remains the most direct manner of ascertaining whether these diseases could have existed.

It is concluded, based on the reconstructions outlined within this thesis, that the climatic and environmental conditions of Franchthi Cave, Nea Nikomedeia and Lerna between the Mesolithic and Late Bronze Age would, theoretically, have supported all three malaria strains and the various *Anopheline* sub-species, and that the malariogenic capacity of these regions was more than sufficient to place an increasingly heavy malarial burden upon these early societies.

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Abbreviations:

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OUP- Oxford University Press

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